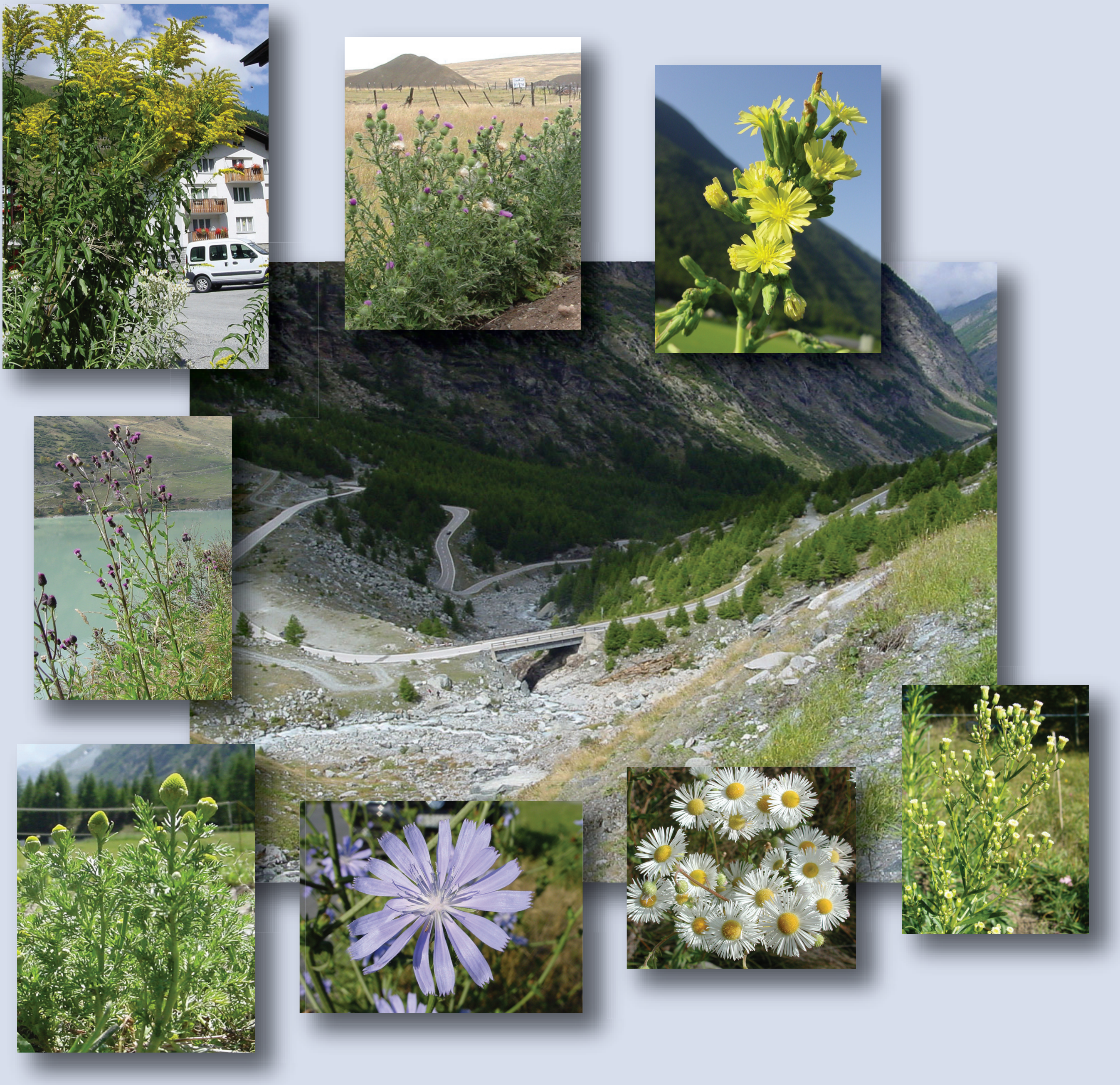
Diss ETH No. 17399

Patterns of distribution and traits of Asteraceae forbs along altitudinal gradients in their native and introduced ranges



Jake Alexander
2007

Diss ETH No. 17399

Patterns of distribution and traits of Asteraceae forbs along altitudinal gradients in their native and introduced ranges

A dissertation submitted to the

SWISS FEDERAL INSTITUTE OF TECHNOLOGY ZURICH

for the degree of

Doctor of Sciences

presented by

JAKE MAXIMILLIAN ALEXANDER

BSc (Hons.) Biological Sciences, Imperial College London

born 17th August 1980

citizen of Great Britain

accepted on the recommendation of

Prof. Peter J. Edwards, examiner
Dr. Hansjörg Dietz, co-examiner
Prof. Antoine Guisan, co-examiner

2007

Contents

Abstract

1. Alien invasive species offer unique opportunities to broaden our knowledge of ecological, biogeographic and evolutionary processes. In particular, the adoption of a comparative approach, studying populations in both their native and introduced ranges, can reveal which factors determine the ability of alien species to spread and invade communities. Such factors include adaptation to changing abiotic conditions, new positive or negative interactions with native species in the introduced range and propagule pressure. However, studies of processes at the invasion front are rarely possible, due to the difficulties of locating the front in heterogeneous landscapes over large spatial scales. We use mountains as model systems to study the spread of alien plant species along environmental (i.e. altitudinal) gradients in the new range. Because the altitudinal limit of an invading species represents an invasion front, an appreciation of the factors determining this limit can reveal the processes underlying invasions in a wider sense. By comparing invasion patterns of eight Asteraceae forb species along altitudinal gradients in their native and introduced ranges in canton Valais (southern Swiss Alps) and the Wallowa Mountains (northeast Oregon, U.S.A.), we aimed to achieve a deeper mechanistic understanding of the factors and processes affecting plant invasions along environmental gradients.

2. A survey of the distribution of these species in roadsides along altitudinal gradients revealed strong similarities in altitudinal distribution patterns between ranges. Furthermore, the maximum observed altitudes were remarkably similar between ranges of most species. This suggests that neither the need to adapt to changing climatic conditions along the gradient nor low propagule pressure has prevented the species from reaching high altitudes in the new range. However, clear region-specific differences in the relative occurrence of alien species in ruderal sites indicate the greater importance of disturbance, probably via release from competition, on invasion patterns.

3. We observed a broad convergence in patterns of quantitative trait variation in natural populations along altitudinal gradients between the native and introduced areas, which also suggests that the need to adapt to changing climatic conditions has not prevented the spread of these species. However, differences in patterns of resource allocation to seeds within capitula suggest that the processes underlying clinal variation in seed size differ between ranges. The importance of region-specific effects (independent of species status) on the strength of clinal patterns of variation indicate the importance of a reciprocal comparative approach to interpret changes in alien plant performance between ranges.

4. Analysis of genetic variation at microsatellite loci within and between populations revealed evidence that the perennial out-crossing *Solidago canadensis* passed through a genetic bottleneck on introduction to the Valais. This was not the case for a second species, the annual autogamous *Lactuca serriola* in the Wallowa Mountains, which was more variable in this region than in the Valais. Reduced genetic variation has apparently had no effect on the altitudinal amplitude of *S. canadensis*, although increasing variation in *L. serriola* might be linked to its wider altitudinal distribution in the Wallowa Mountains.

5. The broad similarity in patterns of trait variation and altitudinal distributions of these alien species, established within c. 100 years of their introduction and despite considerable changes in patterns of genetic variation, are consistent with theories of niche conservatism. Thus although adaptive changes might occur in the new range (e.g. along altitudinal gradients), these appear to be rather confined to the limits of the fundamental niche. Potential exceptions are *L. serriola* and *Cichorium intybus*. Overall, the results of this thesis suggest that biotic interactions with native species, especially competitors, exert a much stronger constraint on the spread of alien species along environmental gradients than changing climatic conditions.

Zusammenfassung

1. Eingeführte invasive Arten bieten einzigartige Möglichkeiten unser Wissen über ökologische, biogeographische und evolutionäre Prozesse zu erweitern. Comparative Ansätze, die Populationen zwischen dem nativen und dem eingeführten Areal untersuchen, sind besonders wertvoll für die Analyse welche Faktoren der Ausbreitungsfähighkeit und Invasibilität eingeführter Arten unterliegen. Solche Faktoren umfassen die Anpassung an veränderte abiotische Bedingungen, neue positive oder negative Interaktionen mit einheimischen Arten im eingeführten Areal und Propagulendruck. Untersuchungen an der Invasionsfront einer Art sind nur selten möglich, da oft keine eindeutige Invasionsfront im heterogenen Landschaftsmosaik zu finden ist. Wir verwenden Gebirge als Modellsysteme um die Ausbreitung von eingeführten Pflanzenarten entlang von Umweltgradienten (in unserem Fall Höhengradienten) im eingeführten Areal zu untersuchen. Weil die Höhengrenze des Areals einer invasiven Pflanzenart im Gebirge eine Invasionsfront darstellt, kann die Analyse der Faktoren, die diese Höhengrenze beeinflussen, Einblicke in generelle, Pflanzeninvasionen fördernde bzw. limitierende Faktoren geben. Wir haben die Invasionsmuster von acht verschiedenen Staudenarten aus der Familie der Asteraceae in ihrem nativen und eingeführten Arealen, in den südlichen Schweizer Alpen (Wallis) und den Wallowa Mountains (OR, USA), untersucht.Unser Ziel war ein vertieftes mechanistisches Verständnis der Faktoren und Prozesse zu erlangen, die Pflanzeninvasionen entlang von Umweltgradienten beeinflussen.

2. In einer Untersuchung im Strassenrandbereich entlang von Höhengradienten waren die Verbreitungmuster der Arten im einheimischen und eingeführten Areal sehr ähnlich. Die höchsten Vorkommen der meisten Arten waren ebenso in beiden Arealen auffallend ähnlich. Diese Ergebnisse deuten darauf hin, dass weder eine Anpassungsnotwendigkeit an sich ändernde klimatische Bedingungen mit der Höhe noch ein niedriger Propagulendruck die Arten daran gehindert haben, auch im eingeführten Areal bis in höher gelegene Gebiete im Gebirge vorzudringen. Klare Unterschiede zwischen den Arealen im relativen Vorkommen der Arten an Ruderalstellen weisen jedoch auf die grosse Bedeutung von Störungen (Verminderung von Konkurrenz) für das Invasionsmuster hin.

3. Wir konnten eine weitgehende Konvergenz in den Mustern quantitativer Merkmale in den untersuchten Populationen der Arten entlang des Höhengradienten beobachten. Dies

ist ein weiterer Hinweis darauf, dass zunehmender Selektionsdruck durch sich ändernde klimatische Bedingungen mit zunehmender Höhe nicht die Ausbreitung der Arten entlang des Gradienten eingeschränkt haben. Unterschiede zwischen den beiden Arealen in der Ressourcenallokation bei Samen innerhalb einzelner Blütenköpfchen weisen aber darauf hin, dass die Prozesse, die der klinalen Variation der Samengrösse unterliegen, zwischen beiden Arealen unterschiedlich sind. Die Bedeutung von regionsspezifischen (arealspezifischen) Einflüssen auf die Stärke klinaler Variationsmuster verdeutlichen die Wichtigkeit des gewählten reziproken Untersuchungsansatzes für die Interpretation von Unterschieden in der Performance der Arten zwischen den Arealen.

4. Die Analyse genetischer Variabilität innerhalb und zwischen Populationen auf der Ebene von Mikrosatelliten ergab Hinweise darauf, dass die fremdbestäubte perenne *Solidago canadensis* bei der Einführung ins Wallis durch einen genetischen Flaschenhals gegangen ist. Für eine zweite Art, die annuelle autogame *Lactuca serriola* war das in den Wallowa Mountains nicht der Fall. Diese Art war im Gegensatz zu *S. canadensis* im eingeführten Areal genetisch sogar variabler als im nativen Areal. Eine reduzierte genetische Variabilität im eingeführten Areal hatte offensichtlich keinen Einfluss auf die Höhenverbreitung von *S. canadensis* im eingeführten Areal. Auf der anderen Seite könnte die höhere genetische Variabilität von *L. serriola* im eingeführten Areal mit ihrer dort besonders breiten Höhenverbreitung in Zusammenhang stehen.

5. Obwohl die Arten erst vor ca. 100 Jahren in ihr neues Areal eingeführt wurden und trotz deutlicher Unterschiede in der genetischen Variablität zeigten sie zwischen den beiden untersuchten Arealen weitgehende Übereinstimmung in ihren Merkmalen und in ihrer Höhenverbreitung. Dies passt zur Theorie der Nischenkonservierung. Obwohl die Arten also in ihrem neuen Areal adaptive Veränderungen zeigen könnten (zB entlang eines Höhengradienten) scheinen sich solche Änderungen mehr oder weniger innerhalb der Grenzen ihrer fundamentalen ökologischen Nische zu ereignen. *L. serriola* und *Cichorium intybus* stellen aber zwei mögliche Ausnahmen dar. Insgesamt weisen die Ergebnisse dieser Doktorarbeit darauf hin, dass biotische Interaktionen mit nativen Organismen im neuen Areal (insbesondere mit Konkurrenten) einen klar stärker limitierenden Einfluss auf die Ausbreitung invasiver Pflanzenarten entlang von Umweltgradienten haben können als sich ändernde klimatische Bedingungen.

General Introduction

This thesis was initiated with the aim of achieving a deeper mechanistic understanding of the processes underlying the spread of alien plant species. In particular, we examine the roles of local adaptation, phenotypic plasticity, propagule pressure and competition as limiting factors of plant invasions, using altitudinal gradients as a model system. These issues are approached experimentally in a complementary thesis of M. Poll. Here I focus on relationships between patterns of distribution of occurrence, trait and genetic variation of eight invasive Asteraceae species along environmental gradients in both their native and introduced ranges. The following discussion relates primarily to plant invasions, although most processes apply equally to invasions by other organisms.

WHAT ARE ALIEN INVASIVE SPECIES?

Essentially, alien invasive species are those which have been deliberately or accidentally introduced by man to new geographic areas, usually very distant from their native range, and are an unavoidable consequence of the globalisation of human societies. Despite over 50 years of interest (Elton 1958), however, authors still differ in their understanding of the term “invasive species” (Richardson et al. 2000). This has probably contributed to a large extent to our limited ability to predict which species are likely to be introduced and succeed in a new area (Davis and Thompson 2000).

Biological invasions can have severe economic and ecological consequences. For example, the annual economic cost of alien species in the U.S.A. has been estimated at US$120 billion (Pimentel et al. 2005). Because of their sometimes disruptive effects on native ecosystem processes and their ability to displace native species, biological invasions have also been listed as the second greatest threat to global biodiversity after habitat loss. Some very prominent species are responsible for considerable damage, and these have attracted substantial attention. For example, invasions of the Eurasian grass *Bromus tectorum* in western North America have replaced millions of hectares of steppe vegetation and have changed the local fire-regime to the detriment of native species (D’Antonio and Vitousek 1992, Novak and Mack 2001). Many authors reserve the term “invasive” for species such as these, which have substantial negative impacts in the new area. However, the vast majority of alien species coexist virtually unnoticed with native species. In this thesis, I prefer the more neutral terms "alien" or "alien invasive" to refer to species which are not native to a given area. I use the term "invasion" to denote the establishment and spread of an alien species in a community/region, without reference to the severity of its ecological consequences (cf. Daehler 2001).

In a community context, all species, whether native or alien, are "invaders", since to persist within a community all must pass the "invasion criterion" of being able to increase when rare (Thompson et al. 1995, Crawley 1997, Shea and Chesson 2002, Silvertown 2005). The tendency to think about invasions as phenomena unique to alien species has led to a divorce of "invasion ecology" from more classical fields of ecology (Davis et al. 2001). However, at a fundamental level, the questions asked by invasion biologists are identical to those asked by many other ecologists (Lodge 1993, Callaway and Maron 2006). For example, both seek to understand why some species are more abundant than others, how they are able to be become established and coexist within communities, how they are able to expand their geographical ranges and how they influence ecosystem processes. More recently, ecologists have increasingly focused on understanding how the diversity and distribution of genetic variation affects ecological processes and to this end biological invasions are emerging as invaluable case studies (Lee 2002, Cox 2004).

HOW DO INVASIONS DIFFER FROM NATURAL RANGE EXPANSIONS?

Natural range expansions, for example the poleward post-glacial recolonisation of temperate species (Hewitt 1996), typically involve spread along an advancing front, so that environmental and biotic conditions should change gradually as the species advances. Whilst technically constituting a form of range expansion, many biological invasions differ in the large geographic scale over which a species is translocated to a new area. Consequently introduced populations are exposed to potentially very different environmental conditions and experience entirely novel interactions with native species in the new range (Alpert 2006, Hallet 2006). In particular, both alien and native species can expose one another to novel allelochemicals (Prati and Bossdorf 2004), a novel competitive environment and new enemies and mutualists. At the same time, aliens are often isolated from their enemies and mutualists in the old range (Keane and Crawley 2002, Facon 2006). In the most part, these altered interactions might be detrimental to the alien, perhaps explaining why so few successfully establish in their new ranges (Williamson and Fitter 1996). Alien populations are often confined to disturbed habitats in the new range, where interactions with neighbouring species (in particular competition) are weakened and resource availability is high and might partly offset any lack of adaptation to prevailing abiotic conditions (Burke and Grime 1996, Davis et al. 2000, Petryna et al. 2002).

Another feature of natural range expansions is that although differentiation between populations tends to increase towards the range margin (Chauvet et al. 2004), marginal populations are (at least indirectly) connected to populations at the core. Populations of alien species, however, are normally isolated from ancestral populations by large geographical distances. In theory, this can have quite substantial effects on the genetics of invading populations. On the one hand, they can be released from the swamping effects of gene-flow from the range core which can stifle emergent adaptations in peripheral populations (Kirkpatrick and Barton 1997, Bridle and Vines 2007, Garant et al. 2007). Founder effects in small establishing populations can also alter the genetic composition of introduced populations relative to the native range. This might especially be the case for species which have a strong genetic structure in the native range, for example highly inbreeding species (Novak and Mack 2005, Taylor and Keller 2007). Coupled with novel selection pressures in the new range, this could lead to rapid evolution in alien populations (Cox 2004).

However, introductions of a given species rarely occur just once, and multiple introductions, or introductions of large numbers of propagules, can lead to high genetic variation within populations (Kolbe et al. 2004). Furthermore, the admixture and intraspecific hybridisation of populations from disparate parts of a species' native range can generate greater variation within introduced populations and create novel genotypic combinations (Ellstrand and Schierenbeck 2000).

WHAT MAKES A SPECIES INVASIVE?

All species are invasive at some level, and given an availability of propagules and a suitable "niche opportunity" they will establish within a community (Shea and Chesson 2002). This explains, at least in part, the general failure to identify specific traits associated with "invasiveness" (Baker 1974, Thompson et al. 1995, Crawley et al. 1996, Sutherland 2004, Muth and Pigliucci 2006). But although in a community context alien species are operationally identical to natives, the fact of their translocation over large distances can explain their sometimes "deviant" behaviour.

In some cases, the success of introduced species might simply be explained by their superior competitive ability (Alpert 2006). This might be due to a general inferiority of native species, for example on islands where competitive interactions between species are hypothesised to be weak (but see Lonsdale 1999). Related to this, alien species might be "pre-adapted" to particular unoccupied niches due to phylogenetic constraint within an invaded area (i.e. particular life-forms never evolved in that area; Mack 2003). Alternatively, they might be pre-adapted to equally alien anthropogenic disturbances in a new range, to which native species are not. This has been suggested especially for Old World species invading agricultural and grazed systems implemented by predominantly European settlers in the New World (di Castri 1989).

Competitive superiority might also result from the novelty of an alien species in the new area. For example, novel attributes such as plant allelochemicals to which native species are not adapted can give alien species a competitive edge ("Novel-weapons" hypothesis; Callaway and Aschehoug 2000). Similarly, they might affect native ecosystem processes in a way which drives systems to an alternative stable state which favours themselves, as in the case of *Bromus tectorum* described above (Simberloff and Von Holle 1999). Perhaps one of the most pervasive explanations for the success of many species is release from "top-down" regulation of population size by specialist enemies in the native range (Keane and Crawley 2002). This can be seen by the sometimes dramatic impact of natural enemies introduced from the native range as biological control agents (e.g. McEvoy et al. 1991, McFadyen 1998).

In all the examples mention above, the success of an alien species can be explained purely by the fact of its introduction to a new area, without recourse to any change in the species itself, i.e. in its ecological behaviour or genetic architecture. However, other theories attribute the success of aliens, at least in part, to evolutionary processes in the new range. For example, evidence suggests that due to release from specialist natural enemies, some alien plants have been selected to reallocate resources from defence to growth ("Evolution of increased competitive ability (EICA)" hypothesis; Blossey and Nötzold 1995). Furthermore, we have seen that considerable changes can occur to the genetic structure of introduced populations. In some cases "invasiveness" has emerged after intraspecific hybridisation among previously isolated populations, or interspecific hybridisation with native and other alien species (Ellstrand and Schierenbeck 2000, Kolbe et al. 2004).

WHAT LIMITS THE SPREAD OF ALIEN SPECIES?

Although the combination of propagule availability and a niche opportunity is sufficient to explain the establishment of any alien species, any (combination) of the processes outlined above can explain the success of an alien species relative to its competitors and relative to its performance in the native range. To this extent they will also dictate its ability to spread across a landscape and invade new communities. However, the relative success of an alien species is also determined by gradients of other factors which limit its spread in a new range. Such gradients might be climatic, such as increasing continentality, latitude or altitude. Alternatively they might be gradients of increasing biotic resistance or decreasing disturbance, as species invade away from sites of initial introduction, where disturbance and propagule pressure are high, into more intact semi-natural vegetation (Dietz and Edwards 2006). Thus in general, invasions along environmental gradients in the new range are limited by (1) the ability of a species to respond to changing abiotic conditions, (2) the outcome of its interactions with the native biota and (3) propagule pressure.

The processes outlined in the previous section relate primarily to biotic interactions among species, in particular with native competitors. It has been shown that the ability of a community to resist invasion, of both native and alien species, is a function of its biodiversity (Kennedy et al. 2002 and references therein, but see Levine 1999, Gilbert and Lechowicz 2005), which is explained largely by niche saturation (i.e. fewer "vacant niches" in diverse communities; Moore et al. 2001, Shea and Chesson 2002, Tilman 2004, Fridley et al. 2007). Thus the relative "invasiveness" of a species will be determined by negative biotic interactions at the invasion front in communities which pose a strong invasion resistance (i.e. are less "invasible"; Crawley 1987, Lonsdale 1999, Blumental 2005, Richardson and Pysek 2006). Consequently the spread of a species along an environmental gradient will be determined in part by the outcome of changing biotic interactions along the gradient (Dietz and Edwards 2006).

The extent of an invasion will also be determined by the ability of the invader to respond to changing abiotic conditions. The success of "weedy" species has been traditionally ascribed to high phenotypic plasticity, which enables them to persist across a wide range of conditions (Baker 1974). However, many studies in more recent years have demonstrated the importance of local adaptation along gradients in the new range (e.g. Lacey 1988, Weber and Schmid 1998, Maron et al. 2004). Thus the ecological amplitude of introduced populations, determined by their plasticity and/or the genetic constraints on their fundamental niche, will delimit the extent of an invasion along an environmental gradient. And because the response to selection is a function of the genetic variation within a population (Futuyma 1998), the particular introduction history of an alien species could determine its ecological amplitude in the new range. Consequently the need for multiple introductions and the time-lag often observed before a species begins to spread might reflect the time required to accumulate sufficient genetic variation and adapt to the new environment (Ellstrand and

Schierenbeck 2000, Kolbe et al. 2004, Dietz and Edwards 2006). Thus the amount of genetic variation contained in invading populations might determine their ability to adapt to changing conditions along environmental gradients and the final extent of the invasion.

A crucial and intuitively obvious determinant of the introduction and initial establishment of an alien species is propagule pressure, a composite measure of the number of introduced propagules and the number of introduction events (Lonsdale 1999, Rouget and Richardson 2003, Colautti et al. 2006). The probability that an invasion is initiated is related to the quantity of introduced propagules, especially if this is sustained over time, to overcome stochastic processes in founder populations (Holt et al. 2005, Von Holle and Simberloff 2005, Colautti et al. 2006). Even for native species, establishment in a community is promoted by additional seed input, suggesting that plant population development in general is dispersal limited (e.g. Tilman 1997, Turnbull et al. 2000).

A thorough understanding of how these factors affect the spread of alien species relies on an appreciation of how they interact (Blumental 2006). For example, biotic interactions will determine the range of environmental conditions a species can tolerate (i.e. its realised niche), and conversely the plasticity/genetic variability of an alien species will dictate the range of communities it can invade. Furthermore, the availability and quantity of introduced propagules will determine the genetic variability of a species and its ability to invade communities.

PLANT INVASIONS ALONG ALTITUDINAL GRADIENTS

In order to gain a mechanistic understanding of the factors limiting plant invasions, it is necessary to examine how causal processes change as an invasion progresses along environmental gradients. For example, in the early stages of an invasion, alien plants might be restricted by the need for disturbance, and consequently their spread is determined largely by dispersal between disturbed sites (propagule pressure) and pre-adaptation to climatic conditions among these sites. However, as an invasion progresses, the species might evolve the ability to invade new habitats and communities, at which point it is constrained more by adaptation and biotic interactions along abiotic and disturbance gradients (Dietz and Edwards 2006). The value of adopting a gradient approach to invasions lies in elucidating the changing importance of any one factor (e.g. changing climatic conditions) relative to others (e.g. propagule pressure, disturbance) along the gradient.

Ultimately, it is necessary to disentangle the causal processes operating at the invasion front. However, it is rarely possible to determine the location of the front over broad spatial scales such as at a continental level. Furthermore, many invasions might already have reached their limits before research into the causal processes can be initiated (Ewel et al. 1999). Along altitudinal gradients, climatic and anthropogenic factors change over small geographic scales, and all species reach their limit at some point along the gradient. Because the altitudinal limit of an invading species represents an invasion front, understanding which factors determine this limit can reveal which factors constrain the invasion process in a more general sense. Mountains thus provide unique opportunities to explore the processes underlying invasions by alien species (Pauchard and Alaback 2004, Arévalo et al. 2005, Becker et al. 2005, McDougall et al. 2005, Parks et al. 2005, Dietz and Edwards 2006).

In temperate areas, increasing altitude is associated with deteriorating conditions for plant growth such as decreases in the length of the growing season coupled with increasing frost and UV exposure (Körner 2003). Human population density also tends to be concentrated at lower altitude, so that anthropogenic disturbances and the introduction of alien propagules associated with them declines towards higher altitudes. Concomitant with this, native species richness decreases with altitude, which has been attributed to the filtering effect of climatic stress, energetic constraints on primary productivity or species-area relationships (Rahbek 1995, Körner 2002, Romdal and Grytnes 2007). Similar patterns have been observed for alien species in temperate regions (Pauchard and Alaback 2004, Becker et al. 2005, McDougall et al. 2005). However, there is also evidence that alien species in Switzerland are extending their altitudinal range upwards (Becker et al. 2005). Thus causal effects in addition to those shaping altitudinal richness patterns of native species might constrain the altitudinal limits of alien species. In particular, Becker et al. (2005) hypothesised that low propagule pressure, biotic resistance from native species and a lack of adaptation to climatic conditions might constrain plant invasions along the gradient.

A comparative approach to invasion biology is required to determine the extent to which patterns of alien species abundance or distribution differ between the native and introduced ranges. This is also prerequisite to an understanding of how and why mechanisms limiting species distributions differ between ranges, and so which factors are responsible for the invasion (Bossdorf et al. 2005, Hierro et al. 2005, Guo 2006). In combination with a reciprocal design (i.e. using reciprocal sets of species native to one area and introduced to the other), this approach also allows an assessment of the system-specificity of invasion patterns, which can provide further insights into factors affecting the invasion process.

OUTLINE OF THE THESIS

This project adopts a reciprocal, comparative approach to the study of plant invasions into two temperate mountain areas, canton Valais in the southern Swiss Alps and the Wallowa Mountains in northeast Oregon, U.S.A.. These regions were chosen for their climatic similarity (see Methods in the following chapters) and because both share a common pool of species native and introduced to each area (Hitchcock and Cronquist 2001, Lauber and Wagner 2001). We focus on eight forb species from one plant family, the Asteraceae, to allow generalisations to be made about the invasion process which are not confounded by phylogenetically determined differences between species. Additionally, the Asteraceae contains a high proportion of alien invasive species and is among the top 20 most "invasive" families worldwide (Pysek 1998). Using this model system, our aim was to understand to what extent plant invasions along altitudinal gradients are limited by changing factors such as climatic conditions and propagule pressure.

In Chapter 1 *Plant invasions along mountain roads: the altitudinal amplitude of alien Asteraceae forbs in their native and introduced ranges* I compare patterns of distribution of occurrences of the eight species in roadside plots and additional disturbed sites along altitudinal gradients. By testing the hypothesis that species have more restricted altitudinal distributions in the introduced range, I aimed to elucidate the role of climatic and dispersal constraints on plant distribution patterns and the effect of disturbance on establishment and spread along the gradient.

In Chapter 2 *Converging responses to altitude in traits of native and introduced Asteraceae forbs* I examine how clinal patterns of variation in growth and reproductive traits along altitudinal gradients vary between the native and introduced ranges of the eight species. The aim was to investigate how the profound changes which can accompany the introduction of a species to a new range are reflected by altered clinal responses to environmental gradients, and to what extent any differences might underlie invasion patterns along these gradients.

In Chapter 3 *Changing patterns of genetic structure and variation during mountain invasions by two Asteraceae forbs* I compare levels and distribution of neutral genetic variation between ranges for a subset of two species, *Lactuca serriola* and *Solidago canadensis*. The aim was to examine to what extent genetic bottlenecks or admixture in the new range, and their associated changes in genetic variation and structure, might have contributed to the observed invasion dynamics of these species. I also discuss the implications of the results for invasions along environmental gradients.

In Chapter 4 *Plant invasions along altitudinal gradients: implications for the evolutionary ecology of alien invasive plants* I first relate the findings to theories of niche conservatism and evolution. I then discuss the implications of this framework for the progression of invasions along environmental gradients.

LITERATURE CITED

Alpert, P. 2006. The advantages and disadvantages of being introduced. Biological Invasions **8**:1523-1534.

Arévalo, J. R., J. D. Delgado, R. Otto, A. Naranjo, M. Salas, and J. M. Fernandez-Palacios. 2005. Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspectives in Plant Ecology, Evolution and Systematics **7**:185-202.

Baker, H. G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics **5**:1-24.

Becker, T., H. Dietz, R. Billeter, H. Buschmann, and P. J. Edwards. 2005. Altitudinal distribution of alien plant species in the Swiss Alps. Perspectives in Plant Ecology, Evolution and Systematics **7**:173-183.

Blossey, B., and R. Nötzold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology **83**:887-889.

Blumental, D. 2005. Interrelated causes of plant invasion. Science **310**:243-244.

Blumental, D. 2006. Interactions between resource availability and enemy release in plant invasion. Ecology Letters **9**:887-895.

Bossdorf, O., H. Auge, L. Lafuma, W. E. Rogers, E. Siemann, and D. Prati. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia **144**:1-11.

Bridle, J. R., and T. H. Vines. 2007. Limits to evolution at range margins: when and why does adaptation fail? Trends in Ecology and Evolution **22**:140-147.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology **77**:776-790.

Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbours: a mechanism for exotic invasions. Science **290**:521-523.

Callaway, R. M., and J. L. Maron. 2006. What have exotic plant invasions taught us over the past 20 years? Trends in Ecology and Evolution **21**:369-374.

Chauvet, S., M. van der Velde, E. Imbert, M. L. Guillemin, M. Mayol, M. Riba, M. J. M. Smulders, B. Vosman, L. Ericson, R. Bijlsma, and B. E. Giles. 2004. Past and current gene flow in the selfing, wind-dispersed species *Mycelis muralis* in western Europe. Molecular Ecology **13**:1391-1407.

Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: A null model for biological invasions. Biological Invasions **8**:1023-1037.

Cox, G. W. 2004. Alien Species and Evolution. Island Press, Washington.

Crawley, M. J. 1987. What makes a community invasible? Pages 429-453 *in* M. J. C. P. J. E. A. J. Gray, editor. Colonization, succession and stability. Blackwell, Oxford.

Crawley, M. J. 1997. Plant Ecology. Blackwell Science, Oxford.

Crawley, M. J., P. H. Harvey, and A. Purvis. 1996. Comparative ecology of the native and alien floras of the British Isles. Philosophical Transactions of the Royal Society of London, B **351**:1251-1259.

D'Antonio, C., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. Annual Review of Ecology and Systematics **23**:63-87.

Daehler, C. C. 2001. Two ways to be an invader, but one is more suitable for ecology. Bulletin of the Ecological Society of America **82**:101-102.

Davis, M., P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.

Davis, M. A., and K. Thompson. 2000. Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. Bulletin of the Ecological Society of America **81**:226-230.

Davis, M. A., K. Thompson, and P. Grime. 2001. Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. Diversity and Distributions **7**:97-102.

di Castri, F. 1989. History of biological invasions with a special emphasis on the Old World. *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological Invasions: A Global Perspective. John Wiley & Sons, Cichester.

Dietz, H., and P. J. Edwards. 2006. Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology **87**:1359-1367.

Ellstrand, N. C., and K. A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proceedings of the National Academy of Science (U.S.A.) **97**:7043-7050.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Metheun, London.

Ewel, J. J., D. J. O'Dowd, J. Bergelson, C. C. Daehler, C. M. D'Antonio, L. D. Gom´ez, D. R. Gordon, R. J. Hobbs, A. Holt, K. R. Hopper, C. E. Hughes, M. LaHart, R. R. B. Leakey, W. G. Lee, L. L. Loope, D. H. Lorence, S. M. Louda, A. E. Lugo, P. B. McEvoy, D. M. Richardson, and P. M. Vitousek. 1999. Deliberate introductions of species: research needs. BioScience **49**:619-630.

Facon, B., Genton, B. J., Shykoff, J., Jarne, P., Estoup, A. & David, P. 2006. A general eco-evolutionary framework for understanding bioinvasions. Trends in Ecology and Evolution **21**:130-135.

Fridley, J. D., J. J. Stachowicz, S. Naeem, D. F. Sax, E. W. Seabloom, M. D. Smith, T. J. Stohlgren, D. Tilman, and B. Von Holle. 2007. The invasion paradox: reconciling pattern and process in species invasions. Ecology **88**:3-17.

Futuyma, D. J. 1998. Evolutionary Biology. 3 edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Garant, D., S. E. Forde, and A. P. Hendry. 2007. The multifarious effects of dispersal and gene flow on contemporary adaptation. Functional Ecology **21**:434-443.

Gilbert, B., and M. J. Lechowicz. 2005. Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. Ecology **86**:1848-1855.

Guo, Q. 2006. Intercontinental biotic invasions: what can we learn from native populations and habitats? Biological Invasions **8**:1451-1459.

Hallet, S. G. 2006. Dislocation from coevolved relationships: a unifying theory for plant invasion and naturalization. Weed Science **54**:282-290.

Hewitt, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnean Society **58**:247-276.

Hierro, J. L., J. L. Maron, and R. M. Callaway. 2005. A biogeographical appraoch to plant invasions: the importance of studying exotics in their introduced *and* native range. Journal of Ecology **93**:5-15.

Hitchcock, C. L., and A. Cronquist. 2001. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Holt, R. D., M. Barfield, and R. Gomulkiewicz. 2005. Theories of niche conservatism and evolution: could exotic species be potential tests? *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species Invasions: Insights into Ecology, Evolution and Biogeography. Sinauer, Sunderland.

Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution **17**:164-170.

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature **417**:636-638.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. The American Naturalist **150**:1-23.

Kolbe, J. J., R. E. Glor, L. R. Schettino, A. C. Lara, A. Larson, and J. B. Losos. 2004. Genetic variation increases during biological invasion by a Cuban lizard. Nature **431**:177-181.

Körner, C. 2002. Mountain biodiversity, its causes and function: an overview. *in* C. Körner and E. M. Spehn, editors. Mountain Biodiversity: a Global Assessment. Parthenon Publishing Group, London.

Körner, C. 2003. Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. 2nd edition. Springer, Berlin.

Lacey, E. P. 1988. Latitudinal variation in reproductive timing of a short-lived monocarp, *Daucus carota* (Apiaceae). Ecology **69**:220-232.

Lauber, K., and G. Wagner. 2001. Flora Helvetica. 3rd edition. Verlag Paul Haupt.

Lee, C. E. 2002. Evolutionary genetics of invasive species. Trends in Ecology and Evolution **17**:386-391.

Levine, J. M. D. A., C. M. 1999. Elton revisited: a review of the evidence linking diversity and invasibility. Oikos **87**:15-26.

Lodge, D. M. 1993. Biological invasions: Lessons for ecology. Trends in Ecology and Evolution **8**:133-137.

Lonsdale. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology **80**:1522-1536.

Mack, R. N. 2003. Phylogenetic constraint, absent life forms and adapted alien plants: a prescription for biological invasions. International Journal of Plant Science **164**:S185-S196.

Maron, J. L., M. Vila, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004. Rapid evolution of an invasive plant. Ecological Monographs **74**:261-280.

McDougall, K. L., J. W. Morgan, N. G. Walsh, and R. J. Williams. 2005. Plant invasions in treeless vegetation of the Australian Alps. Perspectives in Plant Ecology, Evolution and Systematics **7**:159-171.

McEvoy, P., C. Cox, and E. Coombs. 1991. Successful biological control of Ragwort, *Senecio jabobaea*, by introduced insects in Oregon. Ecological Applications **1**:430-442.

McFadyen, R. E. C. 1998. Biological control of weeds. Annual Review of Entomology **43**:369-393.

Moore, J. L., N. Mouquet, J. H. Lawton, and M. Loreau. 2001. Coexistence, saturation and invasion resistence in simulated plant assemblages. Oikos **94**:303-314.

Muth, N. Z., and M. Pigliucci. 2006. Traits of invasives reconsidered: phenotypic comparisons of introduced invasive and introduced noninvasive plant species within two closely related clades. American Journal of Botany **93**:188-196.

Novak, S. J., and R. N. Mack. 2001. Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (Cheatgrass). BioScience **51**:114-122.

Novak, S. J., and R. N. Mack. 2005. Genet bottlenecks in alien plant species: influence of mating systems and introduction dynamics. *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species Invasions: Insights into Ecology, Evolution and Biogeography. Sinauer, Sunderland, Massachusetts.

Parks, C. G., S. R. Radosevich, B. A. Endress, B. J. Naylor, D. Anzinger, L. J. Rew, B. D. Maxwell, and K. A. Dwire. 2005. Natural and land-use history of the Northwest mountain ecoregions (USA) in relation to patterns of plant invasions. Perspectives in Plant Ecology, Evolution and Systematics **7**:137-158.

Pauchard, A., and P. B. Alaback. 2004. Influence of elevation, land use and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. Conservation Biology **18**:238-248.

Petryna, L., M. Moora, C. O. Nunes, J. J. Cantero, and M. Zobel. 2002. Are invaders disturbance limited? Conservation of mountain grasslands in central Argentina. Applied Vegetation Science **5**:195-202.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics **52**:273-288.

Prati, D., and O. Bossdorf. 2004. Allelopathic inhibition of germination by Alliaria petiolata (Brassicaceae). American Journal of Botany **91**:285-288.

Pysek, P. 1998. Is there a taxonomic pattern to plant invasions? Oikos **82**:282-294.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography **18**:200-205.

Richardson, D. M., and P. Pysek. 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography **30**:409-431.

Richardson, D. M., P. Pysek, M. Rejmanek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalisation and invasion of alien plants: concepts and definitions. Biodiverstiy and Distributions **6**:93-107.

Romdal, T. S., and J.-A. Grytnes. 2007. An indirect area effect on elevational species richness patterns. Ecography **30**:440-448.

Rouget, M., and D. M. Richardson. 2003. Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. American Naturalist **162**:713-724.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution **17**:170-176.

Silvertown, J. 2005. Demons in Eden. Chicago University Press, Chicago.

Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions **1**:21-32.

Sutherland, S. 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. Oecologia **141**:24-39.

Taylor, D. R., and S. R. Keller. 2007. Historical range expansion determines the phylogenetic diversity introduced during contemporary species invasion. Evolution **61**:334-345.

Thompson, K., J. G. Hodgson, and T. C. G. Rich. 1995. Native and alien invasive plants: more of the same? Ecography **18**:390-402.

Tilman, D. 1997. Community invasibility, recruitment limitation and grassland biodiversity. Ecology **78**:81-92.

Tilman, D. 2004. Niche tradeoffs, neutrality and community structure: a stochastic theory of resource competition, invasion and community assembly. Proceedings of the National Academy of Sciences (U.S.A.) **101**:10854-10861.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos **88**:225-238.

Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology **86**:3212-3218.

Weber, E., and B. Schmid. 1998. Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. American Journal of Botany **85**:1110-1121.

Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology **77**:1661-1666.

Chapter 1

Plant invasions along mountain roads: the altitudinal amplitude of alien Asteraceae forbs in their native and introduced ranges.

Jake M. Alexander[1], Bridgett Naylor[2], Myriam Poll[1], Peter J. Edwards[1], Hansjörg Dietz[1]

[1]Institute of Integrative Biology, ETH Zürich, Universitätsstrasse 16, 8092 Zürich, Switzerland
[2]USDA Forest Service, Pacific Northwest Research Station, La Grande, OR 97850 U.S.A.

Abstract

Studying plant invasions along environmental gradients is a promising approach to dissect the relative importance of the multiple interacting factors which affect the spread of a species in a new range. Here we report on a survey of the distribution of eight Asteraceae forbs along mountain roads in both their native and introduced ranges in the Valais (southern Swiss Alps) and the Wallowa Mountains (northeast Oregon, U.S.A.). We hypothesised that a lack of adaptation to high altitude conditions and more limiting propagule pressure at higher altitudes in the new range would restrict the altitudinal distribution of aliens relative to the native range. However, all but one of the species reached the same or even higher altitudes in the new range. Thus neither the need to adapt to changing climatic conditions nor lower propagule pressure at higher altitudes appear to have prevented the altitudinal spread of these species in the new range. However, clear region-specific differences in the relative occurrence of alien species in ruderal sites indicate the greater importance of disturbance, probably via release from competition, on invasion patterns. We conclude that human disturbance and competition with the native vegetation might be more important than changing climatic factors for restricting the spread of alien plants along environmental gradients.

Keywords: Plant invasions, environmental gradients, niche conservatism, spatial distribution, roadside ecology.

INTRODUCTION

Many factors are known to influence plant invasions, but syntheses of how and under what circumstances particular factors drive or limit invasions are only beginning to emerge (e.g. Davis et al. 2000, Arim et al. 2005, Blumental 2006, Hallet 2006). The spread of a species in a new range is limited by propagule pressure, abiotic factors and biotic interactions with competitors, enemies and mutualists, and all these factors may vary along environmental gradients such as latitude, continentality and altitude (Dietz and Edwards 2006, Hallet 2006). Species responses to changing conditions along these gradients can be characterised by high phenotypic plasticity (Parker et al. 2003, Richards et al. 2006) or local adaptation (e.g. Lacey 1988, Weber and Schmid 1998) or both.

Along altitudinal gradients, many factors change simultaneously across rather small geographical scales (Arévalo et al. 2005, Becker et al. 2005). Of particular importance for plant species, mean temperatures and the length of the growing season decrease, whilst UV intensity increases at higher altitudes (Körner 2003). Furthermore, the intensity and impact of human activities, which are often associated with high propagule pressure, is much reduced at higher altitudes (Parks et al. 2005). Because populations close to the altitudinal limit of an alien species represent an invasion front, understanding what determines this limit can reveal which factors have the strongest influence on the progress of an invasion. For example, Becker et al. (2005) proposed that the strong decrease in numbers of alien plant species with altitude in the Swiss Alps might be due to a lack of adaptation of invading populations to changing climatic conditions along altitudinal gradients. However, this pattern might also be explained by low propagule pressure, which has emerged as a major determinant of invasion success at both small (e.g. Von Holle and Simberloff 2005) and large (e.g. Rouget and Richardson 2003) spatial scales (Colautti et al. 2006).

One way to investigate the relative importance of climatic factors from other factors such as propagule pressure and biotic interactions is to study the distribution of alien plants along mountain roads. In mountainous regions, climatic conditions change sharply from low to high altitude, whilst habitat factors (e.g. vegetation characteristics, disturbance) along a roadside often remain relatively constant. Mountain roadsides are also punctuated along their length by ruderal sites more disturbed than the normal verge (e.g. settlements, commercial centres, car-parks etc.), and these may be important both as sources of propagules and for facilitating establishment (Marcus et al. 1998, Johnston and Pickering 2001, Godfree et al. 2004). Thus, roads serve not only as conduits for the dispersal of alien species (Tyser and Worley 1992, Parendes and Jones 2000, Johnston and Johnston 2004, Christen and Matlack 2006) but provide a habitat that is typically both disturbed and nutrient-rich, both of which promote the establishment of alien (and native) species (Burke and Grime 1996, Davis et al. 2000).

To take full advantage of investigations into plant invasion processes along environmental gradients in mountains, it is necessary to compare the distributions of alien species in both the native and introduced ranges. Such comparisons can help determine how distributions, and the factors which underlie them, are altered in the new range, and so clarify the processes responsible for the spread of alien species (Bossdorf et al. 2005, Hierro et al. 2005). Furthermore, a reciprocal approach using species both native and introduced to each of the study areas can reveal the relative importance of region-specific effects on invasion patterns.

So far, few studies have compared the response of alien invasive species to environmental gradients in both their native and introduced ranges (Maron et al. 2004). Here we report on a reciprocal study of the distribution of eight species of Asteraceae forbs in roadside verges and ruderal sites. We hypothesised that due to low propagule pressure and a lack of adaptive/plastic responses to high altitude conditions, plants show a more restricted altitudinal distribution in the introduced range. Because of this, the establishment of alien plants, particularly at high altitude, will be restricted to ruderal sites that provide not only more propagules but also offer refuge from competition with natives (Petryna et al. 2002). We also investigated to what extent region-specific effects, such as those due to different management practices or histories of plant introductions, influence the extent and pattern of plant invasions into mountains.

MATERIALS AND METHODS

Species

We selected eight forb species from the Asteraceae - four native to Europe but invasive in North America (*Cirsium arvense*, *Cirsium vulgare*, *Cichorium intybus* and *Lactuca serriola*), and four native to North America but invasive in Europe (*Conyza canadensis*, *Erigeron annuus*, *Matricaria discoidea* and *Solidago canadensis*; Table 1). Except for *S. canadensis*, all species are found in both study areas. The *Solidago canadensis* complex is taxonomically difficult: according to the most recent revision (Semple and Cook 2006), the taxon occurring in the Wallowa Mountains is *S. lepida* whereas that found in Europe is *S. canadensis*, a native of eastern North America. Nonetheless, although the two taxa are now recognised as separate species, they are closely related within the same species complex.

Study systems

The study was conducted in canton Valais in southern Switzerland (46°10'N, 7°20'E), and in the Wallowa Mountains in northeast Oregon, U.S.A. (45°15'N, 117°20'W), two mountain areas with similar temperate, continental climates. Annual precipitation is somewhat higher in the Valais (1060 vs. 744 mm mean annual precipitation) and is distributed more evenly over the year than in the Wallowas, where most rain and snow falls in winter and spring. Variations in mean monthly temperatures are greater in the Wallowas, with mean minimum temperatures on average 1.4°C cooler and maximum temperatures 2.7°C warmer in the Wallowas. However, the climate of the Valais has become slightly warmer and drier in recent years (Rebetez and Dobbertin 2004). (Climatic data are means of four (Valais) and three (Wallowa Mountains) weather stations at comparable altitudes; <http://www.meteoschweiz.ch>, <http://www.wrcc.dri.edu>.) Heat sum (degree days ≥ 5°C) over the growing season decreases similarly with altitude in both systems although the Wallowas have on average 5.3 frost days more during this period than the Valais (see Chapter 2).

Table 1. Geographic and life-history characteristics of the study species.

Species	Origin	Perenniality	Breeding System	Introduction to study area
Cirsium arvense (L.) Scop.	Eurasia	Perennial	Out., Veg.	c. 1900*
Cirsium vulgare (Savi) Ten.	Eurasia	Biennial	Mixed	c. 1900*
Cichorium intybus L.	Europe	Perennial	Out.	c. 1900*
Lactuca serriola L.	Eurasia	Annual	Mixed	c. 1900*
Conyza canadensis (L.) Cronq.	N. America	Annual	Mixed	Since 1800†
Erigeron annuus (L.) Pers.	N. America	Annual	Apomictic	Since 1928‡
Matricaria discoidea DC.	N. America	Annual	Selfing	1914†
Solidago canadensis L.	N. America	Perennial	Out., Veg.	1948†

*See text; †Hegi (1979); ‡ Hess et al. (1972). "Out.", outcrossing; "veg", vegetative.

Parts of the Wallowas are used for cattle ranching and timber extraction, but most of the area has been designated as National Wilderness. The montane zone (c. 1000–1900 m a.s.l.) of the Wallowas is dominated by *Pinus ponderosa* and *Pseudotsuga menziesii* forest and the subalpine forest (c. 1900–2400 m a.s.l.) by *Larix occidentalis and Abies lasiocarpa*, with the true alpine zone beginning at around 2500 m a.s.l. (Pohs 2000, Parks et al. 2005). Lower altitudes (< c. 1000 m a.s.l.) are dominated by sagebrush (*Artemisia* spp.) steppe with agriculture and cattle ranching in the valleys surrounding the central massif (Parks et al. 2005).

The Valais is more densely populated than the Wallowas, with industry, agriculture, tourism and settlement in nearly all of the side valleys leading to the central Rhône valley. The main valley bottom and sides from c. 400–900 m a.s.l. are dominated by settlements, agriculture and viniculture on all but the steepest slopes. The continental mountain belt (c. 900–1900 m a.s.l.; Landolt and Urbanska 2003) consists of a patchwork of agriculture/pasture (21%), forest (60%; dominated by *Pinus sylvestris*) and urban areas (6.5%; Glenz et al. 2001). *P. sylvestris* is replaced by *Picea abies*, *Pinus cembra* and *Larix decidua* at higher altitudes (c. 1900–2400 m a.s.l.), with shrub communities giving way to the alpine zone above c. 2400 m a.s.l. (Landolt and Urbanska 2003). The alpine zone is impacted by tourism, sheep grazing and the ski-infrastructure in some areas.

In each of the two mountain areas, seven roads were chosen which had a wide altitudinal range and were frequently used by traffic. In the Valais, two of the roads sampled link the main valley to major passes (Furka and Grand-St.-Bernard passes), two end at dams (Stausee Mattmark and Barage de Moiry) and the remaining three end at alpine villages (Arolla, Planachaux and Fafleralp; Fig. 1). All these roads are heavily used and have settlements and centres of commerce along their lengths. The roadside vegetation comprises native and alien ruderal species. The latter have presumably been introduced accidentally by traffic and industrial activities or as garden escapes. Roadside verges are mown at regular intervals during the summer.

The road system in the Wallowas was constructed primarily to service mining activities in the mountains around the turn of the 20th century (Pohs 2000), and now mainly provides access for trail-heads and campsites. All the roads sampled except the upper part of the Mount Howard road are open to motor vehicles (Fig. 1). These roads are more highly connected than in the Valais, and the ends of the roads are in some cases spurs of the main road servicing facilities at the locally highest points. Two roads end at fire towers (Mount Harris Loop and Fish Lake Road), three at trail heads (Lostine River, Elkhorn Scenic Byway and Wallowa Mountain Loop) and two at mountain summits (Moss Springs Road and Mount Howard). Most roads in the mountains are gravel, which may be graded annually but otherwise receive little maintenance. Only the Elkhorn Scenic Byway and Wallowa Mountain Loop are paved along most of their length. The former is the only sampled road to be located outside of the Wallowas, across the valley in the neighbouring Elkhorn Range (Fig. 1). The roadside vegetation comprises a mixture of native and alien shrubs, grasses and forbs. Some of the alien species were probably introduced accidentally and have established since the road network was constructed, while others were present in seed mixtures used to stabilise slopes during road construction or as forage species for livestock (Dyrness 1975).

Data collection

Between July and August 2005 in the Valais, and August and September 2006 in the Wallowas, we sampled each road from bottom to top using plots placed at 25 m altitudinal increments. The top of the road was defined as it's highest point and the bottom as its junction with the main road network surrounding the mountains, where there were no appreciable changes in altitude over small spatial scales. Plots of 150 x 2 m were placed along the verge on the right-hand-side of the road, with the outside edge running parallel to the first occurrence of the vegetation on the verge. Within each plot, we recorded the presence/absence of the target species, the amount of tree canopy closure (<33%, 33-66%, >66%) and the dominant vegetation type within 10 m of the road. Species abundance was scored as either low (≤ 10 individuals/ramets) or high (> 10 individuals/ramets). Altitudes were measured and at the end of each transect a waypoint recorded using a Garmin eTrex Legend® hand-held GPS device. In total 378 verge plots were sampled in the Valais, and 296 in the Wallowas.

We also sampled a number of ruderal sites (Valais, 265 sites; Wallowas, 139 sites) located along the right-hand-side of each road. These sites, which included car parks, road-servicing areas, small industrial areas/yards, waste areas, trail heads and campsites, were generally more disturbed than the roadside verges. They were sampled by searching an area of up to 300 m^2, though many sites were smaller than this (Valais, 165; Wallowas, 106). Small sites in the Valais were located on average 127 m higher than normal-sized sites (Student's t = 2.24, df = 258, $P < 0.05$), although there was no significant difference between the mean altitudes of the two types of site in the Wallowas (Student's t = -1.69, df = 135, $P > 0.09$).

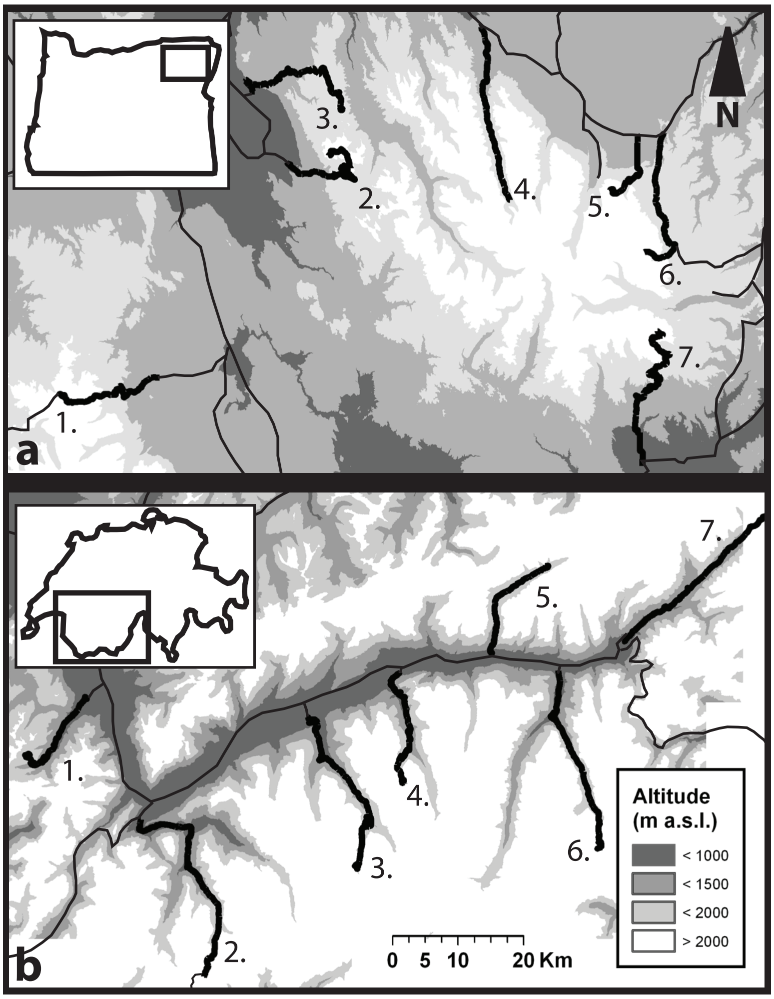


Fig. 1. Topographic maps of the two study areas with the major-road system (surveyed sections shown in bold). In (a; Wallowa Mountains), the roads are (1) the Elkhorn Scenic Byway, (2) Moss Springs road, (3) Mount Harris Loop, (4) Lostine River road, (5) Mount Howard road, (6) Wallowa Mountain Loop and (7) Fish Lake road. In (b; Valais), the roads link the Rhone valley to (1) Planachaux, (2) the Grand-St.-Bernard pass, (3) Arolla, (4) the Moiry dam, (5) Fafleralp, (6) the Mattmark dam and (7) the Furka pass. Note the full extent of road (7) is not shown. Reproduced by permission of swisstopo (BA071648).

In a separate survey conducted in 2006 (June in the Valais, August/September in the Wallowas) to compare species occurrences at and away from the roadside, eleven transects were stratified evenly by altitude along three roads in each system (Valais: roads to Grand-St.-Bernard, Arolla, Stausee Mattmark; Wallowas: Mount Harris Loop, Moss Springs road, Fish Lake road). Each transect consisted of one 2 x 12.5 m plot set out along the roadside, and four 5 x 5 m plots away from the road at 10, 50, 100 and 200 m. Additional plots at 100 m increments up to 500 m from the roadside were sampled for 14 transects in the Valais and

22 in the Wallowas, giving in total 206 plots in the Valais (33 roadside, 173 non-roadside) and 224 in the Wallowas (33 roadside, 191 non-roadside). The occurrence of the target species as well as habitat and vegetation characteristics and the location (GPS) were recorded in each plot as described above.

Data analysis

ALTITUDINAL DISTRIBUTION

All analyses were performed using R (R Foundation for Statistical Computing, version 2.4.0 for Mac OS X). We used mixed-effects multiple logistic regression models (Venables and Ripley 2002) to investigate the relationship between altitude and species occurrence and differences in plant responses along the altitudinal gradients between the native and introduced ranges. Models were fitted containing altitude and its second order polynomial, range and their interaction for each species separately, with road nested in range as random effects. Residuals of these models were tested for spatial autocorrelation, which can bias parameter estimates (Dormann 2007). However, spatial autocorrelation of residuals was weak and because models accounting for this correlation structure were qualitatively unchanged from the non-spatial models, only results of the latter are reported. Because many populations of *M. discoidea* at low altitude in the Valais had already senesced when the survey was conducted, all data below 1000 m a.s.l. were excluded from analyses of this species in the Valais. And because *E. annuus* was only recorded four times in the Wallowas, this species was excluded from all analyses for this region. Trends in the relative abundance of species with altitude in each range were explored by calculating the proportion of plots in which a species was present in high abundance for 200 m altitudinal intervals.

The maximum altitude reached by each species in each region was recorded in three ways: (1) the absolute maximum, (2) the mean of the maximum altitudes along each of the seven roads and (3) the maximum altitude predicted from logistic regression models for the effect of altitude on species occurrence. The latter was defined as the altitude at which the probability of finding a species had declined to 10% of its maximum, and so reduced the influence of outlier populations outside of the "normal" altitudinal range of the species (Becker et al. 2005). Where species occurrence showed a "humped" relationship with altitude, only occurrences above the peak abundance were considered for this calculation.

A bootstrapping procedure was used to investigate whether the higher maximum altitude of *L. serriola* in the Wallowas could be explained by its higher overall frequency of occurrence in this region. Occurrences in the Wallowas were resampled (1000 permutations) to decrease the overall frequency to that in the Valais. The predicted maximum altitude in the Valais was then compared to the null distribution of predicted maximum altitudes from the Wallowas assuming equal frequencies of occurrence.

The degree to which species occurrences were aggregated along roads was described using Pearson's correlation coefficient between matrices of resemblance and Euclidean distance between all pairs of plots. Pairs were described as either different (one contains a presence, the other an absence of a given species) or identical (both contain presences or absences; Legendre and Legendre 1998). Separate matrices were constructed for each region, at low and high altitude, for roads in which the species occurred at least five times.

Table 2. The maximum altitudes and frequency of occurrences within their altitudinal extent attained by the study species in each range. The predicted (pred.) maximum altitude is the altitude at which the probability of occurrence declines to 10% of its maximum (see text). The mean maximum is the mean of the observed (obs.) maxima along each surveyed road. Also shown Pearson's correlation coefficients (*r*) between distance and the occurrence of species in pairs of plots at low and high altitude.

			Maximum altitude				
Species	**Range**	**Freq.**	**Obs.**	**Mean**	**Pred.**	**r (low)**	**r (high)**
Cirsium arvense	Native	0.32	2090	1803	2107	0.01	0.06
	Introduced	0.52	2187	1951	2400	0.12	0.05
Cirsium vulgare	Native	0.09	1826	1516	2252	-0.02	0.08
	Introduced	0.36	2092	1864	2163	0.07	0.09
Cichorium intybus	Native	0.12	1506	991	1185	0.13	0.20
	Introduced	0.13	1753	1450	1394	0.13	0.19
Lactuca serriola	Native	0.27	1401	1153	1292	0.02	-0.02
	Introduced	0.44	1861	1717	1849	0.20	0.07
Conyza canadensis	Native	0.12	1788	1428	1660	0.30	0.21
	Introduced	0.29	1800	1385	1490	0.04	0.09
Erigeron annuus	Native	0.04	1269	1116	NA	NA	NA
	Introduced	0.10	1223	895	909	-0.08	0.09
Matricaria discoidea	Native	0.08	2187	1701	5502	0.09	0.00
	Introduced	0.23	2197	1803	2681	NA	0.03
Solidago	Native	0.14	2160	1899	NA	0.11	0.14
	Introduced	0.07	1530	1096	1456	NA	0.32

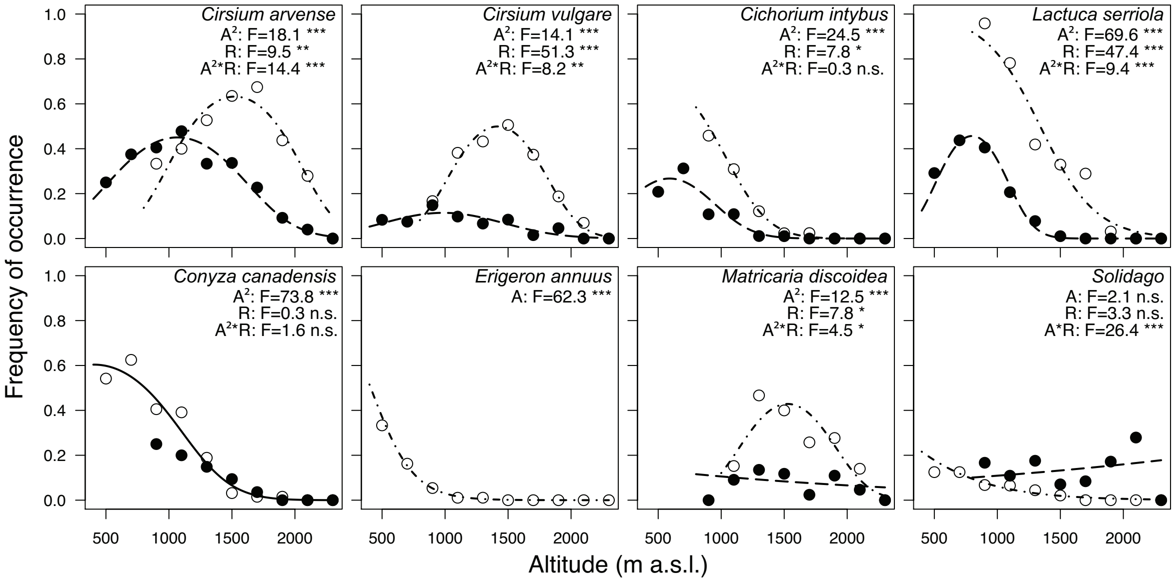


Fig. 2. Relationship between altitude and species occurrence in the native (closed circles, dashed regression lines) and introduced (open circles, dot-dashed regression lines) ranges. Denominator degrees of freedom are 12 for the effects of range (R). For the effects of altitude (A) and A x R, degrees of freedom are 884 for M. discoidea, 635 for E. annuus (introduced range only; see text) and 1062 for all other species. * *P*<0.05; ***P*<0.01; ****P*<0.001; "n.s." not significant.

OCCURRENCE IN RUDERAL SITES AND AWAY FROM ROADSIDES

Vegetation types in the Valais were classed as "open" (e.g. meadow/pasture), "closed" (e.g. forest, shrubland) and "urban" (e.g. towns/villages, industrial complexes). Forest habitat dominated the roadside in the Wallowas, but the canopy cover varied greatly: forest with <33% canopy closure above the roadside was classified as "open", and >33% closure as "closed". Vegetation classes in the Wallowas thus comprised "closed" (closed forest) and "open" vegetation (open forest, grassland habitats and urban areas).

Multiple logistic regression models were fitted to investigate the effects of site characteristics on the occurrence of each species in each region separately. Occurrence was fitted as a function of altitude and its second order polynomial, plot type (verge plot or ruderal site), the dominant vegetation type adjacent to the road, the interaction of transect type with altitude and road as a block effect with no interactions (Newman 1997). The approximate size of the plot (equal to or less than 300 m^2) was included as a covariate to control for its potential confounding effect on species occurrence. Models for which the dispersion parameter (residual deviance/residual degrees of freedom) was not approximately equal to one were refitted using a quasibinomial link function, which estimates the scale parameter by dividing the Pearson χ^2 by the degrees of freedom (Crawley 2002). The results of the quasibinomial models are reported only when they differed qualitatively from the binomial models. Variable selection was performed by elimination of non-significant terms from the full model based on χ^2 at $P<0.05$, or with F-tests in the case of quasibinomial models (Crawley 2002).

The degree of invasion of these species away from the roadside was assessed by comparing occurrences in plots along transects extending into semi-natural vegetation. Because species occurrences were very low (range 0–10% across the whole dataset), native and alien species were pooled and plots were scored for the presence/absence of at least one of the four species from each group. For the same reason, plots were classed simply as roadside/non-roadside without considering the distance of plots from the road. Mixed-effects logistic regression models were fitted with occurrences of native/alien species in each range separately as response variables, dependent on altitude of the roadside plot, plot type (roadside or not) and their interaction, with plot type nested in transect as the random components.

RESULTS

Distribution patterns along altitudinal gradients

Many species were present over the entire altitudinal gradient, and although they generally decreased in occurrence with altitude, most peaked at intermediate altitudes in both the introduced and native ranges (Fig. 2; significant polynomial effects of altitude). This was most pronounced for the two *Cirsium* species and for *Matricaria discoidea* in the Valais, which peaked between 1000–1500 m a.s.l.. *Cichorium intybus*, *Conyza canadensis* and *Lactuca serriola* in the Valais also all peaked in occurrence between 500–1000 m a.s.l. (Fig. 2). For all European natives, the altitude of peak occurrence was shifted upwards in the introduced range by up to 500 m, although there were no consistent differences between ranges for the North American species (Fig. 2). The rate of change in occurrence with altitude was not significantly different in either range for *C. canadensis* and *C. intybus* (Fig. 2). All species were more frequent in the introduced range, irrespective of the mountain region, apart from *Solidago* which was more frequent in the native range (Table 2, Fig. 2). On average, alien plant species were more frequent in the Wallowas (average 32% of plots) than in the Valais (14% of plots).

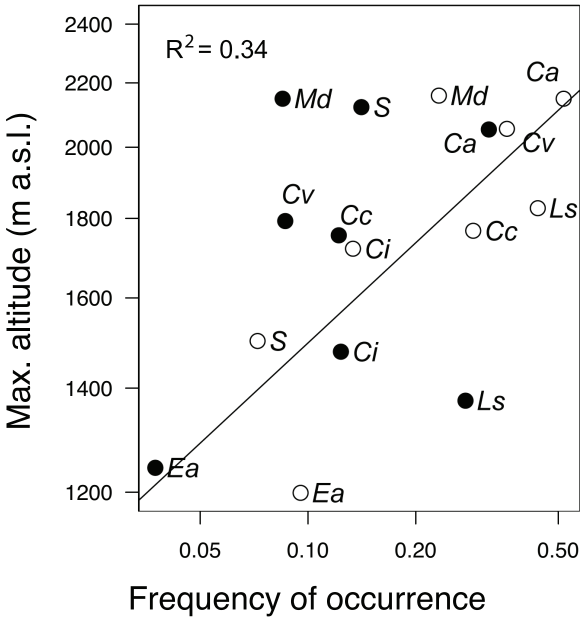


Fig. 3. The maximum observed altitude of a species as a function of its frequency within its altitudinal extent in the native (filled circles) and introduced (open circles) ranges (log scales). "*Ca*", *C. arvense*; "*Cv*", *C. vulgare*; "*Ci*", *C. intybus*; "*Ls*", *L. serriola*; "*Cc*", *C. canadensis*; "*Ea*", *E. annuus*; "*Md*", *M. discoidea*; "*S*", *Solidago*.

Across all species and in both ranges, the (log) maximum altitude reached by a species was positively related to its (log) frequency within the altitudinal range over which it occurred ($F_{1,12}$ = 5.1, *P* < 0.05; Fig. 3). All European species reached higher absolute maximum and mean maximum altitudes across the seven roads in the introduced range (Student's t = 2.89–6.88, d.f. = 11–12, *P* < 0.05). However, this was not statistically significant for *C. arvense* (Student's t = 1.30, d.f. = 12, *P* = 0.22; Table 2), whilst the predicted maximum altitude of *C. vulgare* was rather higher in the native range. The predicted maximum altitude of *L. serriola* in the native range (1292 m a.s.l.; Table 2) was significantly lower than the predictions of the resampled data (one-sided 95% CI = 1730 m a.s.l.) and so cannot be explained purely by its lower frequency of occurrences in this region. The maximum altitudes of the North American species were not significantly different in either range (Student's t = 0.27–1.34, d.f. = 7–12, *P* > 0.22), apart from *Solidago* which reached a higher maximum in the native range (Student's t = 4.58, d.f. = 12, *P* < 0.001). The predicted maximum altitudes of *C. intybus*, *L. serriola* (native range only), *C. canadensis* and *E. annuus* were substantially lower than the observed maxima, indicating that high-altitude occurrences are outliers to the core distribution of these species.

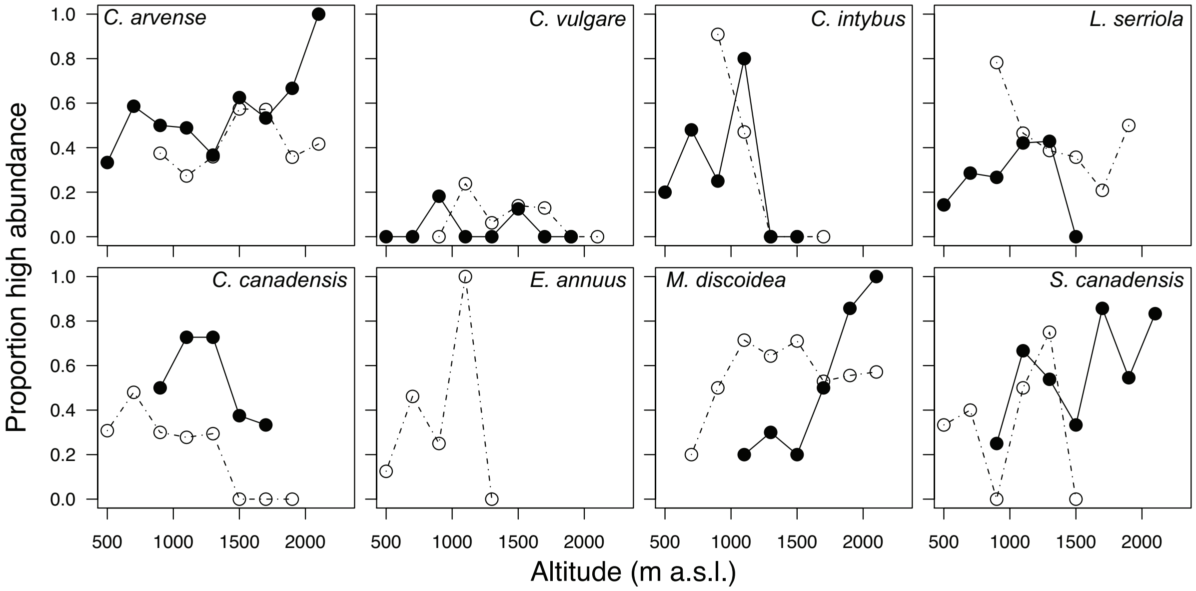


Fig. 4. Relationship between species abundance (proportion of high-abundance occurrences in 200 m altitudinal intervals) and altitude in the native (filled circles joined by solid lines) and introduced (open circles joined by broken lines) ranges.

The correlations between species occurrences in plots and the distance between them were generally weak, with the exceptions of *C. intybus*, *C. canadensis* and *Solidago*. Occurrences of the European species were generally more aggregated (larger *r*) at low altitudes in the introduced range, whilst there were only small differences between ranges at high altitudes (Table 2). Occurrences of *C. canadensis* were substantially more aggregated in the native range, and in the introduced range of *Solidago* (Table 2). Overall there was no tendency for occurrences to be more aggregated at high than at low altitude.

For a few species (*C. arvense* and *M. discoidea* in both ranges, *Solidago* in the native range), relative abundance - measured as the proportion of high-abundance occurrences in 200 m intervals - tended to increase with altitude; in contrast, the relative abundance of *C. canadensis* decreased with altitude in both ranges. The remaining species (*C. vulgare*, *E. annuus*, *C. intybus*, *L. serriola* and *Solidago*) showed no consistent trends with altitude between ranges (Fig. 4). However, where relative abundance did not generally decrease with altitude (*L. serriola*, *E. annuus* and *Solidago*, all in the Valais), the species were still only present in low abundance at high altitude.

Table 3. Minimal logistic regression models of the effect of altitude (A), plot type (P) and vegetation type (V) on species occurrence, using elimination of non-significant terms based on χ^2 at $P<0.05$. All models contain road as a block factor and plot size as a covariate (not shown). D^2 is the percentage of variation explained by the model.

Species	Range	Model components	Deviance		Resid. d.f.	D^2
			Null	Resid.		
Cirsium arvense	Native	$-A^2$, V	784	661	626	15.7
	Introduced	$-A^2$	600	514	423	14.4
Cirsium vulgare	Native	–A, V	331	307	627	7.2
	Introduced	$-A^2$, V	551	471	422	14.5
Cichorium intybus	Native	–A, V	351	230	627	34.5
	Introduced	$-A^2$, P, V, A^2 x P	271	154	419	43.4
Lactuca serriola	Native	$-A^2$, P	551	339	627	38.4
	Introduced	–A, V	560	363	423	35.1
Conyza canadensis	Native	–A, V*	257	180	423	29.9
	Introduced	$-A^2$, P, V, A^2 x P	696	402	623	42.2
Erigeron annuus	Native	NA	NA	NA	NA	NA
	Introduced	–A, P	224	124	628	44.6
Matricaria discoidea	Native	P, V	243	202	423	17.1
	Introduced	$-A^2$, P, V	559	340	448	39.3
Solidago	Native	P	345	304	424	11.7
	Introduced	–A, P, V	236	174	626	26.3

*Factor significant in quasibinomial model after correction for under-dispersion (see text).

Species occurrences in ruderal sites and away from roadsides

Alien species were much more frequent in ruderal sites in the Valais than in the Wallowas. In the Valais, all four North American species were significantly more frequent in ruderal sites than in less disturbed verge plots (Fig. 5; Table 3). In contrast, the occurrence of all species native to the Valais (except *L. serriola*) were independent of ruderal sites (Fig. 5, Table 3). In the Wallowas, only *M. discoidea* was more frequent in ruderal sites, whilst *Solidago* was significantly more frequent in verge plots. For most species, the relative effect of ruderal sites on species occurrence did not change along the altitudinal gradients. In their introduced ranges, *C. intybus* was relatively more frequent, and *C. canadensis* less frequent, in ruderal sites at higher altitudes (significant interactions of altitude x plot type; Table 3).

In both regions, alien species tended to occur more frequently in plots adjacent to open/urban vegetation, whilst native species were generally more frequent adjacent to closed vegetation (Table 3). This was true for the introduced *C. canadensis*, *M. discoidea* and *Solidago* in the Valais, and is consistent with their higher occurrence in ruderal sites. Conversely, the European natives *C. arvense*, *C. vulgare* and *C. intybus* were significantly more frequent adjacent to closed vegetation. In the Wallowas, the native species *C. canadensis* and *M. discoidea* and the introduced *C. vulgare* were more frequent adjacent to closed vegetation, whilst the alien species *C. intybus* and *L. serriola* were more frequent adjacent to open vegetation. Both alien and native species were much more common in plots at the roadside than away from it ($F_{1,31} = 11.0–26.5$, $P < 0.001$; Table 4). However, aliens in the Wallowas invaded twice as many plots (16%) away from the road than aliens in the Valais (8%; Table 4).

DISCUSSION

Converging responses to altitude between ranges

As species invade a new range, they must overcome several hurdles including dispersal limitation, biotic resistance from resident species and lack of adaptation to abiotic conditions (Richardson et al. 2000, Dietz and Edwards 2006). This resistance to invasion is likely to be especially strong towards higher altitudes in mountains, with their steep environmental gradients and generally low human disturbance. However, our expectation that in the new range these plant species would therefore be more restricted in the maximum altitude they reached is clearly not substantiated by our data. Almost all species reached a mean maximum altitude that was either higher in the introduced range or not different from that in the native range. Furthermore, the similar altitudinal patterns of occurrence and relative abundance between ranges suggest that these species are no more limited by climatic factors associated with altitude in the introduced than in the native range. The establishment of these invasion patterns in less than 100 years since introduction indicates that the species are either highly plastic in their introduced range (e.g. Williams et al. 1995, Parker et al. 2003, Baret et al. 2004) or have adapted rapidly to high-altitude conditions (e.g. Lacey 1988, Weber

Table 4. Percentage of plots occupied by the eight Asteraceae species in transects extending away from the roadside into semi-natural vegetation.

Status	**Valais**		**Wallowas**	
	Roadside	**Surrounding**	**Roadside**	**Surrounding**
Native	32	12	15	4
Introduced	50	8	45	16

and Schmid 1998, Sexton et al. 2002, Maron et al. 2004). Only *Solidago* showed substantial differences between ranges, which might be attributable to taxonomic differences between the species in the Wallowas and the Valais, or because it was the only species to be more frequent in the native range (see below).

The convergence of distribution patterns in both native and introduced areas resemble converging patterns of variation in quantitative traits of these species along altitudinal gradients (Chapter 2), as has been shown for other alien species in response to latitude (Huey et al. 2000, Maron et al. 2004). Other studies have found alien species to occupy similar climatic envelopes in both the native and introduced areas (e.g. Wester and Juvik 1983, Wilson et al. 1992, Ullmann et al. 1995, Arévalo et al. 2005, but see Broennimann et al. 2007). These observations suggest that species niches are usually conserved between ranges (Holt et al. 2005, Wiens and Graham 2005, Parmesan 2006), despite the profound ecological (e.g. biotic interactions, selection pressures) and genetic (e.g. admixture, gene flow) changes that can accompany a species on introduction to a new area which is isolated from the ancestral range (Lee 2002, Levine 2003, Holt et al. 2005).

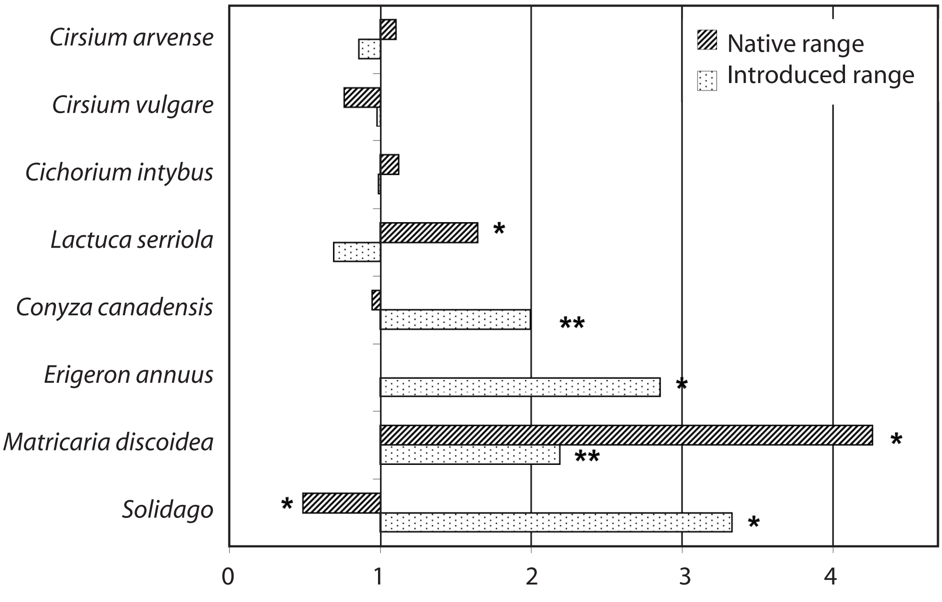


Fig. 5. Ratio of species occurrence in ruderal sites and verge plots. Values greater than one indicate species occur more frequently in ruderal sites. An asterisk indicates a significant relationship between plot type and species occurrence in multiple logistic regression models (* $P<0.05$, ** $P<0.001$; see text; Table 3).

The patterns of distribution of these species along altitudinal gradients fall into two groups that are independent of the origin of the species. One group of species (*Cirsium arvense*, *C. vulgare*, *Solidago* and *Matricaria discoidea*) occurred over a broad altitudinal range, peaking at intermediate altitudes where environmental conditions were presumably most favourable for their growth (cf. Arévalo et al. 2005). A second group of mainly annual species (*Conyza canadensis, Erigeron annuus, Lactuca serriola* and *Cichorium intybus*) had more restricted altitudinal distributions in both the native and introduced ranges, with the highest occurrences consisting only of scattered individuals. High altitude conditions are unfavourable for annual species, which constitute <2% of the total alpine flora (Körner 2003), and annual invaders may be unable to complete their life cycles during the short growing season (Trtíková et al., unpublished data). The upland occurrences we observed might constitute sink populations maintained primarily by dispersal from low altitude (Pulliam 1988). We would therefore expect perennial species, and especially clonal plants such as *C. arvense* and *Solidago*, to be more successful invaders of high altitudes. However, the success of annual species such as *M. discoidea* might be explained by a rapid life-cycle and low stature, by which they are uncoupled from adverse climatic conditions at high altitudes (Körner 2003, Poll et al., unpublished data).

Propagule pressure and altitudinal limits

The occurrence of these species at similar altitudes in both ranges and at similar levels of relative abundance, indicates that their spread to high altitudes in the new range has also not been affected by low propagule pressure. Indeed, the higher maximum altitudes of the European species in the Wallowas might be partly driven by a higher propagule pressure in this region where they are on average nearly twice as frequent (Levin 2006, Wilson et al. 2007). Evidence for dispersal limitation (or a lack of "safe sites" for establishment) might be found in the more aggregated occurrences of the European species at low altitude in the Wallowas (Dormann 2007). However, overall these limitations appear to be no more acute in the introduced than in the native range. It could be that propagule pressure is most important in the early stages of an invasion when a species is not yet in equilibrium with its (abiotic) environment.

The higher maximum altitudes reached in the Wallowas by two European species, *C. intybus* and *L. serriola*, could not be explained by differences in their frequency of occurrences (i.e. a sampling effect) between regions. A likely explanation is that the climatic envelope they can tolerate is shifted upwards in the Wallowas compared to the Valais (cf. Broennimann et al. 2007). This might be due to broad differences in regional climate, which would also explain the upward shift in the altitude of peak occurrence of the other European species. However, if climatic differences were responsible we would also expect the North American species to have higher maxima in the Wallowas, which is not the case. Alternatively, suitable microsites for establishment at high altitude might be more abundant in the Wallowas, for example due to the greater openness of the roadside vegetation (Poll et al., unpublished manuscript).

The ability of plant populations to respond to selection is dependent on the amount of genetic variation within them (Futuyma 1998). It is thus conceivable that *C. intybus* and *L. serriola* have a broader altitudinal tolerance in the Wallowas than in the Valais due to higher genetic variation within and across populations, either because they are an admixture of multiple introductions or stem from an area of the native range more variable that the Valais. In support of this hypothesis, populations of *L. serriola* in the Wallowas were found to have significantly greater diversity at seven microsatellite loci than Valais populations (Chapter 3).

System specificity of invasion patterns

Differences in introduction history might partly explain why the frequency of occurrence of alien species in the Wallowas was more than twice that in the Valais. Deliberate introductions of European species to North America have been sustained by a much greater propagule pressure, and their spread has been nurtured by management practices (e.g. mowing and cattle-grazing) to which they are pre-adapted (di Castri 1989, Mack and Erneberg 2002). Multiple introductions from different source areas have also generated high genetic diversity in populations of some of these species (e.g. Neuffer and Hurka 1999, Novak and Mack 2005). Many North American species have also been introduced deliberately to Europe, but mainly as ornamentals (e.g. *Solidago* spp.; Weber and Schmid 1998, *E. annuus*; Hegi 1979) without intensive propagation and deliberate dispersal.

The success of Old World species in North America has also been explained by the paucity of native ruderal species (di Castri 1989). This, and regional differences in land-use and disturbance regimes, might be reflected in the clear regional differences we observed in the importance of ruderal sites for alien plants. By reducing competition with the native vegetation, disturbance promotes the establishment of aliens, perhaps explaining why aliens in the Valais are restricted to ruderal sites. The verges are typically composed of dense stands of native agricultural weeds and meadow species that may also be adapted to local management practices, in particular mowing (Baker 1974), to which the aliens are not. In the Wallowas, management by grading of the roads, logging and cattle-grazing activities cause more soil disruption and vegetation openness, so that establishment of mainly alien, ruderal species is promoted along the length of roads and not just in ruderal sites. This might partly explain why the Wallowas are more highly invaded than the Valais, both at and away from the roadside. In line with this, seedling establishment of these species was shown to be positively related to disturbance in the Valais, but not in the Wallowas where all experimental plots were open and rather disturbed (Poll et al., unpublished manuscript, but see Paiaro et al. 2007).

At least some of the observed differences between the Valais and Wallowas might be due to traits of the species themselves. For example, the North American species have smaller seeds than the European species (Chapter 2); and because seed size affects the success of seedling establishment (Moles and Westoby 2004), they might be more limited by disturbance (Burke and Grime 1996, Poll et al., unpublished manuscript).

Implications for plant invasion along altitudinal gradients

Our data suggest that whilst niche boundaries provide the fundamental constraints to invasion (e.g. the altitudinal limit), changing conditions along environmental gradients within the niche have apparently not hindered the spread of Asteraceae forb species into higher mountains in the introduced area. This is either because invading populations are highly plastic or are able to adapt rapidly to local environmental conditions. Thus climatic factors are likely to pose only transitory and limited constraints to spread along environmental gradients, although this might be contingent on the genetic variability or plasticity within populations at the invasion front. To what extent ecological amplitude is underpinned by levels of genetic variability in invading populations remains to be determined. However, this result implies that the decrease in numbers of alien species with altitude observed in most temperate mountain systems is explained by an absence of mountain plants in the alien flora, rather than a reduced ability of invaders to adapt to changing climatic conditions (Becker et al. 2005). The high frequency of occurrence of these species in their new range indicates that propagule pressure is also probably most important only at the early stages of an invasion when the species is scarce, i.e. at the invasion front.

Disturbance, most likely through a release from competition with native vegetation, has emerged as the most important determinant of distribution patterns along the gradients in this study (Johnston and Pickering 2001, Godfree et al. 2004). The relative importance of ruderal sites as refugia from biotic/climatic constraints and sites of high propagule/nutrient availability generally did not change along the altitudinal gradients (cf. Petryna et al. 2002). However, our data suggest that plant invasions along environmental gradients are likely to be more constrained by changing patterns of disturbance and biotic interactions (i.e. competition with native vegetation) than by climatic factors, given sufficient plasticity/genetic variation in invading populations. This is likely to be especially the case for invasions advancing into less disturbed semi-natural vegetation (Dietz and Edwards 2006). Experiments manipulating competition and climatic factors are now needed to test this prediction. However, the greater altitudinal amplitude of *L. serriola* and *C. intybus* in the introduced range raises the intriguing possibility that novel evolution could enable introduced populations to invade environments outside the niche constraints existing in the native range (Ellstrand and Schierenbeck 2000, Broennimann et al. 2007).

ACKNOWLEDGMENTS

We thank Catherine Parks and the La Grande Forestry and Range Sciences Laboratory for providing support in the Wallowa Mountains, and Sabine Guesewell and Kirk Moloney for statistic advice. Josephine Haase, Susan Geer and Christoph Kueffer kindly helped with fieldwork. This project was financed by a grant of the Swiss National Science Foundation to HD.

LITERATURE CITED

Arévalo, J. R., J. D. Delgado, R. Otto, A. Naranjo, M. Salas, and J. M. Fernandez-Palacios. 2005. Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspectives in Plant Ecology, Evolution and Systematics **7**:185-202.

Arim, M., S. R. Abades, P. E. Neill, M. Lima, and P. A. Marquet. 2005. Spread dynamics of invasive species. PNAS **103**:374-378.

Baker, H. G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics **5**:1-24.

Baret, S., S. Maurice, T. Le Bourgeois, and D. Strasberg. 2004. Altitudinal variation in fertility and vegetative growth in the invasive plant *Rubus alceifolius* (Rosaceae), on Réunion island. Plant Ecology **172**:265-273.

Becker, T., H. Dietz, R. Billeter, H. Buschmann, and P. J. Edwards. 2005. Altitudinal distribution of alien plant species in the Swiss Alps. Perspectives in Plant Ecology, Evolution and Systematics **7**:173-183.

Blumental, D. 2006. Interactions between resource availability and enemy release in plant invasion. Ecology Letters **9**:887-895.

Bossdorf, O., H. Auge, L. Lafuma, W. E. Rogers, E. Siemann, and D. Prati. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia **144**:1-11.

Broennimann, O., U. A. Treier, H. Müller-Schärer, W. Thuiller, A. T. Peterson, and A. Guisan. 2007. Evidence of climatic niche shift during biological invasion. Ecology Letters **10**:701-709.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology **77**:776-790.

Christen, D., and G. Matlack. 2006. The role of roadsides in plant invasions: A demographic approach. Conservation Biology **20**:385-391.

Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: A null model for biological invasions. Biological Invasions **8**:1023-1037.

Crawley, M. J. 2002. Statistical Computing: an Introduction to Data Analysis using S-Plus. Wiley, Chichester.

Davis, M., P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.

di Castri, F. 1989. History of biological invasions with a special emphasis on the Old World. *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological Invasions: A Global Perspective. John Wiley & Sons, Cichester.

Dietz, H., and P. J. Edwards. 2006. Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology **87**:1359-1367.

Dormann, C. F. 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. Global Ecology and Biogeography **16**:129-138.

Dyrness, C. T. 1975. Grass-legume mixtures for erosion control along forest roads in western Oregon. Journal of Soil and Water Conservation **30**:169-173.

Ellstrand, N. C., and K. A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proceedings of the National Academy of Science (U.S.A.) **97**:7043-7050.

Futuyma, D. J. 1998. Evolutionary Biology. 3rd edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Glenz, C., A. Massolo, D. Kuonen, and R. Schlaepfer. 2001. A wolf habitat suitability prediection study in Valais (Switzerland). Landscape and Urban Planning **55**:55-65.

Godfree, R., B. Lepschi, and D. Mallinson. 2004. Ecological filtering of exotic plants in an Australian sub-alpine environment. Journal of Vegetation Science **15**:227-236.

Hallet, S. G. 2006. Dislocation from coevolved relationships: a unifying theory for plant invasion and naturalization. Weed Science **54**:282-290.

Hegi, G. 1979. Illustrierte Flora von Mitteleuropa. Paul Parey, Berlin.

Hierro, J. L., J. L. Maron, and R. M. Callaway. 2005. A biogeographical appraoch to plant invasions: the importance of studying exotics in their introduced *and* native range. Journal of Ecology **93**:5-15.

Holt, R. D., M. Barfield, and R. Gomulkiewicz. 2005. Theories of niche conservatism and evolution: could exotic species be potential tests? *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species Invasions: Insights into Ecology, Evolution and Biogeography. Sinauer, Sunderland.

Huey, R. B., G. W. Gilchrist, M. L. Carlson, D. Berrigan, and L. Serra. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science **287**:308-310.

Johnston, F. M., and S. W. Johnston. 2004. Impact of road disturbance on soil properties and on exotic plant occurence in subalpine areas of the Australian Alps. Arctic, Antarctic and Alpine Research **36**:201-207.

Johnston, F. M., and C. M. Pickering. 2001. Alien plants in the Australian Alps. Mountain Research and Development **21**:284-291.

Körner, C. 2003. Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. 2nd edition. Springer, Berlin.

Lacey, E. P. 1988. Latitudinal variation in reproductive timing of a short-lived monocarp, *Daucus carota* (Apiaceae). Ecology **69**:220-232.

Landolt, E., and K. M. Urbanska. 2003. Our Alpine Flora. SAC Publications, Frutigen.

Lee, C. E. 2002. Evolutionary genetics of invasive species. Trends in Ecology and Evolution **17**:386-391.

Legendre, P., and L. Legendre. 1998. Numerical Ecology. Elsevier, Amsterdam.

Levin, D. A. 2006. Ancient dispersals, propagule pressure and species selection in flowering plants. Systematic Botany **31**:443-448.

Levin, D. A. 2003. The ecological transition in speciation. New Phytologist **161**:91-96.

Mack, R. N., and M. Erneberg. 2002. The United States naturalized flora: largely the product of deliberate introductions. Annals of the Missouri Botanical Garden **89**:176-189.

Marcus, W. A., G. Milner, and B. Maxwell. 1998. Spotted Knapweed distribution in stock camps and trails of the Selway-Bitterroot Wilderness. Great Basin Naturalist **58**:156-166.

Maron, J. L., M. Vila, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004. Rapid evolution of an invasive plant. Ecological Monographs **74**:261-280.

Moles, A., and M. Westoby. 2004. Seedling survival and seed size: a synthesis of the literature. Journal of Ecology **92**:372-383.

Neuffer, B., and H. Hurka. 1999. Colonization history and introduction dynamics of *Capsella bursa-pastoris* (Brassicaceae) in North America: isozymes and quantitative traits. Molecular Ecology **8**:1667-1681.

Newman, J. A., Bergelson, J. & Grafen, A. 1997. Blocking factors and hypothesis testing in ecology: is your statistics text wrong? Ecology **78**:1312-1320.

Novak, S. J., and R. N. Mack. 2005. Genet bottlenecks in alien plant species: influence of mating systems and introduction dynamics. *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species Invasions: Insights into Ecology, Evolution and Biogeography. Sinauer, Sunderland, Massachusetts.

Paiaro, V., A. Mangeaud, and E. Pucheta. 2007. Alien seedling recruitment as a response to altitude and soil disturbance in the mountain grasslands of central Argentina. Plant Ecology, published online.

Parendes, L. A., and J. A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conservation Biology **14**:64-75.

Parker, I. M., J. Rodriguez, and M. E. Loik. 2003. An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. Conservation Biology **17**:59-72.

Parks, C. G., S. R. Radosevich, B. A. Endress, B. J. Naylor, D. Anzinger, L. J. Rew, B. D. Maxwell, and K. A. Dwire. 2005. Natural and land-use history of the Northwest mountain ecoregions (U.S.A.) in relation to patterns of plant invasions. Perspectives in Plant Ecology, Evolution and Systematics **7**:137-158.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics **37**:637-669.

Petryna, L., M. Moora, C. O. Nunes, J. J. Cantero, and M. Zobel. 2002. Are invaders disturbance limited? Conservation of mountain grasslands in central Argentina. Applied Vegetation Science **5**:195-202.

Pohs, K. 2000. The Wallowa Mountains: A Natural History Guide. Northwest Mountain Works, Portland.

Pulliam, H. R. 1988. Sources, sinks and population regulation. The American Naturalist **132**:652-661.

Rebetez, M., and M. Dobbertin. 2004. Climate change may already threaten Scots pine stands in the Swiss Alps. Theoretical and Applied Climatology **79**:1-9.

Richards, C. L., O. Bossdorf, N. Z. Muth, J. Gurevitch, and M. Pigliucci. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters **9**:981-993.

Richardson, D. M., P. Pysek, M. Rejmanek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalisation and invasion of alien plants: concepts and definitions. Biodiverstiy and Distributions **6**:93-107.

Rouget, M., and D. M. Richardson. 2003. Inferring process from pattern in plant invasions: a semi-mechanistic model incorporating propagule pressure and environmental factors. American Naturalist **162**:713-724.

Semple, J. C., and R. E. Cook. 2006. Asteraceae. Pages 151-157 Flora of North America Editorial Committee, eds 1993+. Flora of North America North of Mexico. 12+ vols., New York and Oxford.

Sexton, J. P., J. K. McKay, and A. Sala. 2002. Plasticity and genetic diversity may allow saltceder to invade cold climates in North America. Ecological Applications **12**:1652-1660.

Tyser, R. W., and C. A. Worley. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). Conservation Biology **6**:253-262.

Ullmann, I., P. Bannister, and J. B. Wilson. 1995. The vegetation of roadside verges with respect to environmental gradients in southern New Zealand. Journal of Vegetation Science **6**:131-142.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. 4th edition. Springer, New York.

Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology **86**:3212-3218.

Weber, E., and B. Schmid. 1998. Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. American Journal of Botany **85**:1110-1121.

Wester, L., and J. O. Juvik. 1983. Roadside plant communities on Mauna Loa, Hawaii. Journal of Biogeography **10**:307-316.

Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: Integrating evolution, ecology and conservation biology. Annual Review of Ecology, Evolution and Systematics **36**:519-539.

Williams, D. G., R. N. Mack, and R. A. Black. 1995. Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. Ecology **76**:1569-1580.

Wilson, J. B., G. L. Rapson, M. T. Sykes, A. J. Watkins, and P. A. Williams. 1992. Distributions and climatic correlations of some exotic species along roadsides in South Island, New Zealand. Journal of Biogeography **19**:183-194.

Wilson, J. R. U., D. M. Richardson, M. Rouget, S. Proches, M. A. Amis, L. Henderson, and W. Thuiller. 2007. Residence time and potential range: crucial considerations in modelling plant invasions. Diversity and Distributions **13**:11-22.

Chapter 2

Converging responses to altitude in traits of native and introduced Asteraceae forbs

Jake M. Alexander[1], Peter J. Edwards[1], Myriam Poll[1], Catherine G. Parks[2], Hansjörg Dietz[1]

[1]Institute of Integrative Biology, ETH Zürich, Universitätsstrasse 16, 8092 Zürich, Switzerland

[2]USDA Forest Service, Pacific Northwest Research Station, La Grande, OR 97850 U.S.A.

ABSTRACT

Due to altered ecological/evolutionary contexts in the new area, we could expect alien plant responses to environmental gradients, revealed through patterns of trait variation, to differ from the native range. In particular, the spread of alien plant species along such gradients might be limited by their ability to establish clinal patterns of trait variation. We investigated trends in growth and reproductive traits in eight alien invasive Asteraceae species along altitudinal gradients in their native and introduced ranges (Valais, Switzerland and Wallowa Mountains, Oregon). Plants responded similarly to altitude in both ranges, being generally smaller and having fewer inflorescences but larger seeds at higher altitudes. However, these trends were modified by region-specific effects that were independent of species status. This suggests that it is not possible to explain any differential performance of alien species in the introduced range without a fully reciprocal approach to test the basis of these differences. Furthermore, we found differences in patterns of resource allocation to capitula among species in the native and the introduced areas. These suggest that the mechanisms underlying trait variation, for example increasing seed size with altitude, might differ between ranges. The overall convergence of patterns of trait variation between ranges indicates that the need to respond to altitudinal gradients in the new range, possibly by local adaptation, has not limited the ability of these species to invade into mountain regions.

Keywords: Alien plant, invasion, seed size, environmental gradient, reciprocal design, Swiss Alps, Wallowa Mountains, niche conservatism.

INTRODUCTION

Plant species introduced into a new range are presented with many challenges. In particular, they encounter novel abiotic and biotic conditions to which they must respond either through local adaptation or by phenotypic plasticity. While earlier work stressed phenotypic plasticity as a key trait enabling some alien species to colonise wide geographic and ecological ranges (e.g. Baker 1974), more recent studies have demonstrated that evolutionary change can also be important (e.g. Lacey 1988, Weber and Schmid 1998, Sexton et al. 2002, Maron et al. 2004). Alien plants often establish in relatively "benign" sites with high anthropogenic disturbance where resistance from native species is low (Dietz and Edwards 2006). However, evolutionary change is likely to be particularly important during the secondary phase of invasion, as species expand their range into less favourable environments, such as into semi-natural habitats or along strong climatic gradients (Dietz and Edwards 2006).

Reproductive traits have an important influence upon the population dynamics of a species and therefore upon its success as an invader (Willis and Hulme 2004, Lloret et al. 2005). And because traits such as seed size often vary along environmental gradients (Baker 1972, Vera 1997, Blionis and Vokou 2002, Moles and Westoby 2003, Murray et al. 2003, Baret et al. 2004), we would expect invasions along these gradients to be associated with clinal variation in reproductive traits. When attempting to predict the potential distribution of an alien species based on its climatic envelope in the native range, it is assumed that species responses to environmental gradients (i.e. their ecological niche) are conserved between ranges (Peterson 2003). However, the failure of some niche-based models to accurately predict species distributions has raised the possibility that species can respond differently in the new range (Fitzpatrick et al. 2007). Populations introduced to a new range can experience profound changes in their biotic interactions (Hallet 2006) and to their abiotic environment and/or genetic architecture (e.g. increasing or decreasing genetic variability, or recombination of genotypes from diverse areas of the native range; Bossdorf et al. 2005). These changes might restrict or induce differences in plant responses to similar environmental gradients between ranges. Comparing patterns of plant trait variation in the native and introduced ranges should thus reveal how the ability of introduced species to respond to environmental gradients might influence their spread in a new range (Maron et al. 2004, Bossdorf et al. 2005, Hierro et al. 2005).

Mountain systems present strong, multidimensional environmental gradients (Körner 2003), and plants at extreme positions along these gradients face very different growth conditions. Not surprisingly, most species are restricted to a more or less well-defined altitudinal range (Blionis and Vokou 2002, Parks et al. 2005), and mountains are therefore excellent model systems for studying plant responses to environmental variation over small geographical scales (cf. Becker et al. 2005, Daehler 2005). Furthermore, an understanding of how the spread of alien species is limited along altitudinal gradients could be extrapolated to other larger-scale environmental gradients such as continentality or latitude.

Recent studies show that rather few alien species occur at higher altitudes in temperate regions (Becker et al. 2005, Parks et al. 2005). While this could be due to a lack of propagule pressure - since human activities tend to be concentrated at lower altitudes - it might also reflect poor adaptation to high-altitude sites. For example, Becker et al. (2005) hypothesise that before they reach mountain areas, populations of alien plant species normally pass through a "low-altitude filter" that excludes high-altitude genotypes. In addition, they suggest that gene flow from low-altitude populations might disrupt emerging adaptations in high-altitude populations. If the altitudinal distribution of aliens is generally limited by a lack of adaptation to high-altitude conditions, we would expect to see differences between the introduced and native ranges in patterns of variation along altitudinal gradients. In particular we would expect traits associated with performance/fitness, such as flower number or plant size, to be more negatively impacted at high altitude in the introduced than in the native range. Furthermore, we would expect clines in potentially adaptive traits (e.g. seed size) observed in the native range to be absent in the introduced range.

Here we present a comparative study of variation in plant traits along altitudinal gradients within natural populations of eight Asteraceae species in their native and introduced ranges in the Swiss Alps and the Wallowa Mountains in Oregon, U.S.A. By using a reciprocal approach we hoped to identify not only any differences in the response of species in their native and introduced ranges, but also to assess whether region-specific factors affected patterns of variation and invasion success. In particular we asked: (1) how do plant traits vary with altitude? (2) do species show similar patterns of trait variation in the native and introduced ranges? (3) do region-specific effects influence patterns of trait variation across all species independently of species status (native or introduced)?

MATERIALS AND METHODS

Species

We selected eight forb species from the Asteraceae - four native to Europe but invasive in North America (*Cirsium arvense*, *Cirsium vulgare*, *Cichorium intybus* and *Lactuca serriola*), and four native to North America but invasive in Europe (*Conyza canadensis*, *Erigeron annuus*, *Matricaria discoidea* and *Solidago canadensis*; Table 1). Except for *S. canadensis*, all species are found in both study areas. The *Solidago canadensis* complex is taxonomically difficult: according to the most recent revision (Semple and Cook 2006), the taxon occurring in the Wallowa Mountains is *S. lepida* whereas that found in Europe is *S. canadensis*, a native of eastern North America (J. Semple, *personal communication*). Nonetheless, although the two taxa are now recognised as separate species, they are assigned to the same species complex and are closely related.

Table 1. Geographic and life-history characteristics of the study species.

Species	Origin	Life history	Breeding System	Highest pop. (m a.s.l.)*		Introduction to study area
				CH	US	
Cirsium arvense (L.) Scop.	Eur.	Perennial	Out., veg.	1980	2170	c. 1900†
Cirsium vulgare (Savi) Ten.	Eur.	Biennial	Mixed	1830	2000	c. 1900†
Cichorium intybus L.	Eur.	Perennial	Out.	1510	1320	c. 1900†
Lactuca serriola L.	Eur.	Annual	Mixed	1400	1860	c. 1900†
Conyza canadensis (L.) Cronq.	N. A.	Annual	Mixed	1490	1580	Since 1800‡
Erigeron annuus (L.) Pers.	N. A.	Annual	Apomictic	1410	1260	Since 1928§
Matricaria discoidea DC.	N. A.	Annual	Selfing	2110	2180	1914‡
Solidago canadensis L.	N. A.	Perennial	Out., veg.	1410	2190	1948‡

*The altitude of highest populations sampled in this study; †see text; ‡Hegi (1979); §Hess et al. (1972). "Eur.", Eurasia; "N. A.", North America; "veg", vegetative; "Out.", outcrossing;.

Study Regions

The study was conducted in the central Alps, in canton Valais in southern Switzerland, and in the Wallowa Mountains in northeast Oregon, U.S.A.. The two mountain areas are of similar size and have similar temperate, continental climates. Annual precipitation is somewhat higher in the Valais and is distributed more evenly over the year than in the Wallowas, where

Table 2. Geographic and climatic characteristics of the study regions.

	Valais, Swiss Alps	**Wallowa Mountains**
Latitude	46°00–46°20	45°00–45°30
Altitude (m a.s.l.)	372–4634	c. 700–3001
Mean Annual Precipitation (mm)	599/1520*	382/1105†
Mean Monthly Temp (°C)	-1.3–18.7/-5.7–9.2*	-2.5–18.9/-7.2–14.4†
Area (km^2)	5224	5285

*Means for low/high altitude weather stations: <www.meteoschweiz.ch> (Sion/Visp (mean 561 m a.s.l.) and Evolène/Grande-St.-Bernard (mean 2149 m a.s.l.), 1961–1990); † <www.wrcc.dri.edu> (La Grande/Enterprise (mean 990 m a.s.l.) and Mt. Fanny (2139 m a.s.l.), 1971–2000).

most rain and snow falls in winter and spring (Table 2). However, the climate of the Valais has become slightly warmer and drier in recent years (Rebetez and Dobbertin 2004). As part of another experiment, temperature loggers ("iButtons", Maxim Integrated Products, Inc.) were placed along two altitudinal transects in both study areas in 2005. Heat sum (degree days ≥ 5°C) over the growing season (April – September) decreased similarly with altitude in both systems (non-significant interaction of altitude x system; $F_{1,8} = 4.35$, $P > 0.07$; Fig. 1a). The number of frost days (min. temperature < 0°C) increased with altitude in both systems (Fig. 1b), but the Wallowas had on average 5.3 frost days more during this period (significant effect of system; $F_{1,8} = 10.38$, $P < 0.05$).

Parts of the Wallowa Mountains are used for cattle ranching and timber extraction, but most of the area has been designated as National Wilderness. The montane zone (c. 1000–1900 m a.s.l.) is dominated by *Pinus ponderosa* and *Pseudotsuga menziesii* forest and the subalpine forest (c. 1900–2400 m a.s.l.) by *Larix occidentalis* and *Abies lasiocarpa*, with the true alpine zone beginning at around 2500 m a.s.l. (Pohs 2000, Parks et al. 2005). Lower altitudes (< c. 1000 m a.s.l.) are dominated by sagebrush (*Artemisia* spp.) steppe with agriculture and cattle ranching in the valleys surrounding the central massif (Parks et al. 2005). The road system, which was constructed around the turn of the 20th century primarily to service mining activities in the mountains (Pohs 2000), now provides access for trail-heads and campsites. Apart from paved roads connecting the settlements below the mountains, most roads in the mountains are gravel, which may be graded annually but otherwise receive little maintenance. The roadside vegetation comprises a mixture of native and alien grasses and forbs. Some of the latter were probably introduced accidentally since the construction of the road network, while others were present in seed mixtures used to stabilise slopes during road construction or as forage species for livestock (Dyrness 1975).

The Valais is more densely populated than the Wallowas, with more industry, agriculture, tourism and settlement in nearly all of the side valleys leading to the central Rhône valley. The main valley bottom and sides from c. 400–900 m a.s.l. are dominated by settlements, with agriculture and viniculture on all but the steepest slopes. The continental mountain belt (c. 900–1900 m a.s.l.; Landolt and Urbanska 2003) forms a broad altitudinal zone consisting of a patchwork of agriculture/pasture (21%), forest (60%; dominated by *Pinus sylvestris*) and urban areas (6.5%; Glenz et al. 2001). *P. sylvestris* is replaced by *Picea abies*, *Pinus cembra* and *Larix decidua* at higher altitudes (c. 1900–2400 m a.s.l.), with shrub communities giving way to the alpine zone above c. 2400 m a.s.l. (Landolt and Urbanska 2003). Apart from limited sheep grazing and the ski-infrastructure in some areas, the alpine zone is largely unaffected

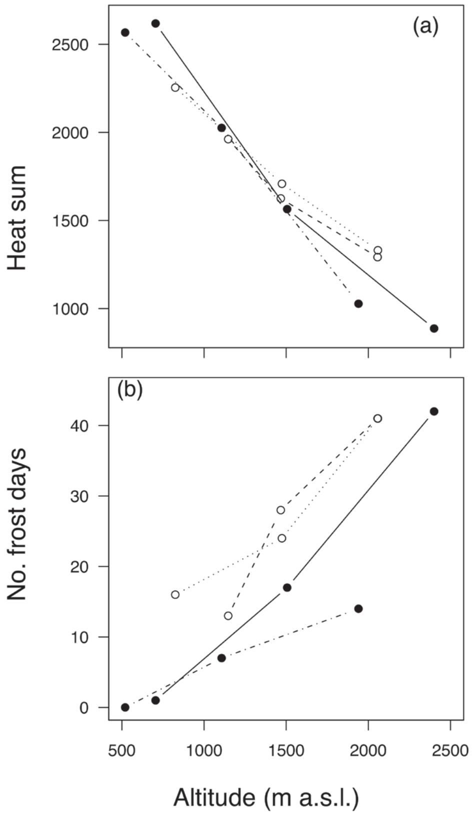


Fig. 1. Relationship between altitude and (a) heat sum (degree days ≥ 5°C) and (b) number of frost days (minimum temperature < 0°C) in the Valais (CH; filled circles) and the Wallowa Mountains (US; open circles) from April to September 2005. The data were collected along four altitudinal transects (roads): Visp to Furka pass (CH; solid line), Martigny to Grand St. Bernard pass (CH; dot-dashed line), Mount Harris Loop (US; dotted line), Moss Springs Rd (US; dashed line).

by human activity. The roads range from major international traffic routes along the valley bottom and across several mountain passes, to small local roads and farm tracks. As in the Wallowas, the roadside vegetation comprises a mixture of native and alien ruderal and meadow species, of which the latter have presumably been introduced accidentally by traffic and industrial activities or as garden escapes. In contrast to the Wallowas, roadsides are mown at regular intervals during the summer.

Population Selection

The distribution and approximate altitudinal limits of the study species in each area were determined during preliminary surveys in July 2004 (Wallowas) and July 2005 (Valais). Based on these, we selected nine to eleven populations of each species that were evenly spaced across their altitudinal range in each region. All populations were sampled primarily from open roadside sites. In the Wallowas, 20 road systems extending from low to high altitudes were sampled, including four towns (containing seven populations), whilst in the Valais 18 road systems were sampled, including 17 towns/villages (containing 33 populations). Because the study areas were rather large (Table 2), populations of a given species were chosen to be as geographically separated as possible to reduce spatial autocorrelation of environmental factors. In the Wallowas, low-altitude populations were mainly sampled on the western side of the mountain range ($F_{3,80} = 11.6$, $P < 0.001$), but there was no tendency to sample populations from similar altitudes within the same geographical area of the Valais ($F_{2,80} = 1.38$, $P > 0.2$; levels are eastern, central and western Valais).

Preference was given to true roadside populations growing along the carriageway, but often it was necessary to sample other disturbed sites such as car parks, yards or industrial fallows to ensure an even altitudinal stratification. In these cases, sites located close to the desired altitude were selected. The non-roadside sites were heterogeneous but tended to be more disturbed by human activity, with populations growing in more open, "ruderal" vegetation. In the Valais a total of 83 populations were sampled, 47 at roadside sites and 36 at other disturbed sites. In total, 84 populations were sampled in the Wallowas, with only eight from non-roadside sites. The mean altitude of populations sampled from roadside sites in the Valais (1227 m a.s.l.) was higher than that from non-roadside sites (906 m a.s.l.; $F_{1,81} = 13.69$, $P < 0.001$), but there was no difference between the two kinds of site in the Wallowas ($F_{1,82} = 1.08$, $P > 0.3$).

Measurement of Plant Traits

Approximately ten (range 5–14) flowering plants per population were sampled between the end of July and the end of September 2004 in the Wallowas, and during the same period of 2005 in the Valais. This extended sampling period was necessary because of the later development of plants at higher altitudes. Because we were only able to sample a few plants per population, we selected the largest individuals. If small populations contain fewer large plants, then the mean size of individuals selected using this criterion would have been affected by the size of the population; however, because population size did not vary significantly with altitude ($F_{2,80} = 1.84, P > 0.1$; Valais, $F_{2,81} = 0.92, P > 0.4$; Wallowas) it could not have confounded the relationship between plant size and altitude.

Total stem height (to the top of the inflorescence), number of stems (excluding clonal species) and total number of capitula were determined for all individuals. It was often not possible to isolate genetic individuals of the clonal species (*C. arvense* and *Solidago*), so measurements were made on individual ramets. Capitula were recorded as either unopened/opened flower heads or as full/empty seed heads. The ratio of unopened/opened capitula to full/empty seed heads was used as an estimate of ontogeny. Capitulum number was counted directly for species with relatively few capitula per plant (*C. arvense*, *C. vulgare* and *M. discoidea*; on main stem only for *E. annuus*). For the remaining species (*C. canadensis*, *C. intybus*, *L. serriola* and *Solidago*), capitulum number was estimated from counts of capitula from three panicles in the inflorescence of the tallest stem.

One to 17 ripe seed heads (or five to 67 for *Solidago*) were collected from each plant. Whenever possible, full seed heads were collected so that the number of seeds per capitulum could be counted. The one-seeded fruits or achenes (referred to hereafter as seeds) were separated from the capitula and air-dried. Of the larger-seeded European species, three to 247 (mean 85) seeds from each plant were counted and weighed. Six to 708 (mean 136) seeds of the smaller-seeded North American species were counted under a dissecting microscope and weighed. When samples contained too many seeds to count by eye, a sub-sample was counted and the seed number in the remainder of the sample was estimated based on its mass. Filled (viable) seed were separated from the samples and re-weighed separately. Viable seed was not weighed separately for the 2004 collections made in the Wallowas. To correct for this, mean viable seed mass and percent viable seed were estimated from pooled seed collections from each population. We then calculated mean (uncorrected) seed mass per population from the original data. The ratio of the two means was applied as a correction factor to all samples per population, and mean percent viable seed was used to estimate viable seed number per head. On average, seed size in the Wallowas was adjusted by a factor of 0.98±0.33 (mean ± 1 SD). Correcting the data did not qualitatively change the effect of altitude on seed size. However, seeds were significantly larger in the Wallowas and in the native range in a model containing uncorrected data ($F_{1,6} = 9.94–12.81$, $P < 0.05$), due to the occasional overestimation of seed size in the Wallowas. Capitulum seed mass was calculated as the product of seed size and number per capitulum.

Statistical Analyses

All analyses were performed in R (R Foundation for Statistical Computing, version 2.4.0 for Mac OS X). To assess patterns of trait variation across all species, data were first standardised by dividing each trait value by the maximum for that species (Legendre and Legendre 1998). We then fitted mixed-effects models for each trait containing species status (native or introduced), region (Valais or Wallowas), altitude, the two-way interactions of altitude with species status and region and their three-way interaction. Populations nested in region nested in species were treated as random effects. Additionally, models were fitted at the species level for each trait, with altitude, region and their interaction as fixed effects and population nested in region as random effects. All models were checked for equal variance and normality of errors. To meet these assumptions, capitulum number was log-transformed.

Because seed size is known to change during ontogeny (Willis and Hulme 2004), ontogeny (see above) was included as a covariate in models of seed size at the species level. Additionally, to control for their possible confounding effects on patterns of trait variation, site type (roadside or not), population size (<10 individuals, 11-100 individuals, >100 individuals) and ontogeny were included as covariates in additional models fitted across all species.

RESULTS

In both regions and across all species, stem height decreased significantly with altitude (Fig. 2a, Table 3). This effect was considerably stronger in the Wallowas than in the Valais (significant interaction of altitude x region; Fig. 2a; Table 3), with an average decrease of 41% between 500 m a.s.l. and 1500 m a.s.l. in the Wallowas compared to a decrease of 10% in the

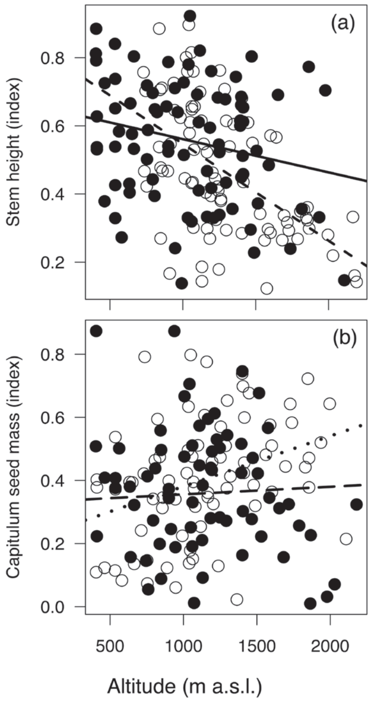


Fig. 2. Relationship between altitude and (a) standardized stem height and (b) standardized capitulum seed mass across all species. In (a), filled circles and the solid regression are for populations in the Valais, open circles with the broken regression line are Wallowa populations. In (b), filled circles with the broken regression line are populations in the native range and open circles with the dotted regression line are introduced populations (see Table 3). Data are population means, but for clarity error bars have been omitted.

Valais. However, there were no significant differences in stem height within species between the native and introduced ranges (non-significant interaction of altitude x status; Table 3), and this pattern did not change depending on the region (non-significant interaction of altitude x region x status; Table 3).

(Log) capitulum number per individual also decreased significantly and substantially with altitude (by an average of 64% between 500 m a.s.l. and 1500 m a.s.l.) for all species apart from *Cirsium arvense* (Fig. 3). Across all species this relationship did not differ between the native and introduced ranges (Table 3). Plants in the Valais had significantly more capitula than those in the Wallowas (Fig. 3; Table 3). For some species, altitude interacted significantly with region (*Cichorium intybus*, *Conyza canadensis* and *Erigeron annuus*), the decline in capitulum number being more pronounced in the Wallowas (significant interactions of altitude x region; Fig. 3, Table 4). This is also reflected in the marginally significant tendency for (log) capitulum number of native species in the Wallowas to decrease more strongly with altitude (interaction of altitude x region x status; Table 3). However, across all species the relationship with altitude was not different depending on region and/or status (non-significant 2-way interactions; Table 3). The main effects of altitude and region on capitulum number can be partly explained by decreasing plant height with altitude, since (log) capitulum number is correlated with height across all species and systems ($r = 0.44$, d.f. = 1611, $P < 0.001$).

Seed size increased with altitude across all species and the relationship did not differ among species between the native and introduced ranges and/or between regions (Table 3). In models fitted at the species level, this relationship was significant for five species, but only *L. serriola* showed significantly different relationships in the native and introduced ranges (Fig. 4; Table 4). Seed size of *C. canadensis* also increased with altitude in the introduced range (Valais; $F_{1,8} = 19.51$, $P < 0.01$), although this was not significant in a model containing data from both ranges (Fig. 4, Table 4). On average, seed mass increased by 39% from 500 m to 1500 m (estimated from a regression of mean seed size on altitude), but the relative increase in seed size was much greater in particular cases; for example, seed size in the Valais populations of *L. serriola* was 106% greater at 1500 m than at 500 m (Fig. 4). Ontogeny had a significantly positive effect on seed size of *L. serriola*, *C. canadensis*, *E. annuus* and *M. discoidea* (Table 4), but including this covariate in the models did not qualitatively change the effect of altitude on seed size.

Table 3. Mixed-effects model (residual maximum-likelihood method) summaries for traits measured in eight Asteraceae forbs in their native and introduced ranges. Degrees of freedom (numerator, denominator) are (1,6) for R and S. For A, A x R and A x S, df are (1,148) for stem height and (log) capitulum number, (1,137) for seed size and (1,125) for capitulum seed mass. Significant terms (P < 0.05) are indicated by bold type.

	Stem height		**(Log) capitulum number**		**Seed size**		**Capitulum seed mass**	
Source	***F***	***P***	***F***	***P***	***F***	***P***	***F***	***P***
Region (R)	**6.92**	0.039	**15.68**	0.008	0.05	0.824	0.03	0.867
Status (S)	0.94	0.370	0.70	0.434	0.48	0.513	1.00	0.355
Altitude (A)	**34.16**	<0.001	**53.36**	<0.001	**33.03**	<0.001	**8.68**	0.004
A x R	**20.46**	<0.001	2.31	0.130	0.52	0.472	<0.01	0.976
A x S	0.08	0.775	<0.01	0.941	0.03	0.860	**4.50**	0.036
A x R x S	0.11	0.737	3.86	0.051	1.74	0.189	0.18	0.672

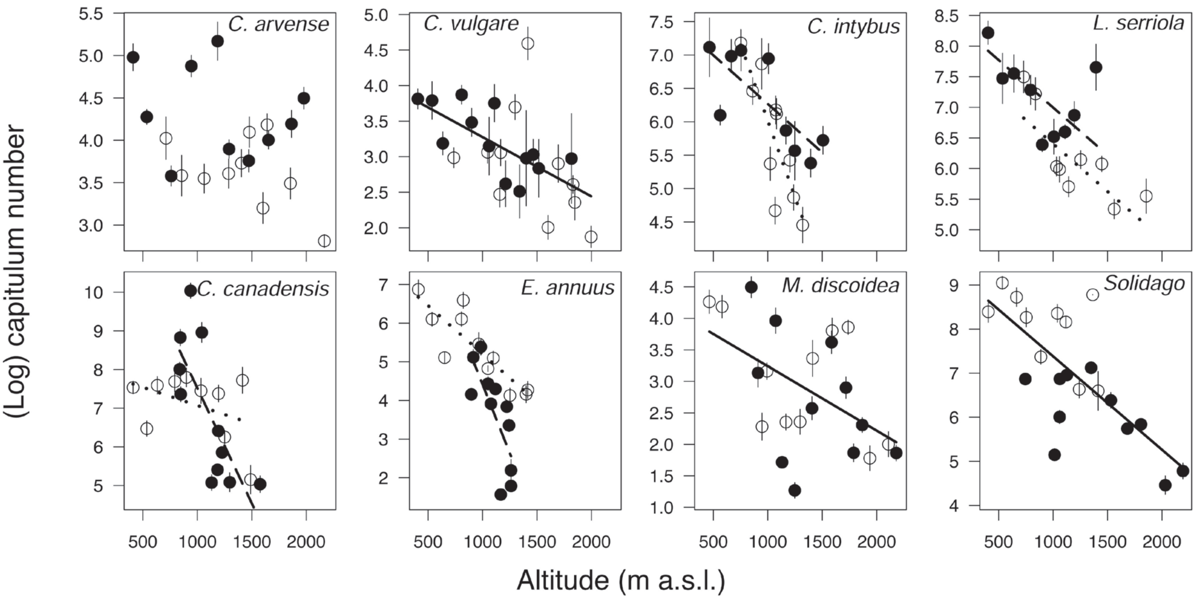


Fig. 3. Relationship between (log) capitulum number and altitude in the native (filled circles) and introduced (open circles) ranges. Solid regression lines are fitted for a significant main effect of altitude on (log) capitulum number ($P < 0.05$; see Table 4). Where altitude interacted significantly with species status, a dashed line is fitted for the relationship in the native range, and dotted line for that in the introduced range. No line is fitted for non-significant effects. The top four species in the panel are native to Europe and the bottom four native to North America. Data are population means with standard errors.

Capitulum seed mass (the product of mean viable seed mass and number of seeds per capitulum) was the only trait to show differences among species between the native and introduced areas (significant interaction of altitude x status; Fig. 2b, Table 3). Models fitted separately for native and introduced populations revealed that in the native range, capitulum seed mass did not vary significantly with altitude ($F_{1,60} = 0.11, P > 0.7$; data not shown) but that it increased significantly with altitude in the introduced range ($F_{1,67} = 16.68, P < 0.001$; data not shown). However, the sample size was not sufficient to detect these differences at the species level, where capitulum seed mass increased significantly with altitude for *E. annuus* and *M. discoidea* only, independently of species status (Appendix 1).

Including site type, population size and ontogeny in models did not qualitatively change the main effects of altitude, status, region and their interactions on seed size and stem height (Appendix 2). (Log) capitulum number was lower, but also declined more strongly with altitude in the Wallowas in this model (significant interaction of altitude x region; $F_{1,129} = 4.36, P < 0.05$; Appendix 2). The interaction of altitude and status on capitulum seed mass was only marginally significant across all populations ($P = 0.078$; Appendix 2). However, in models fitted for native/introduced populations separately, the positive effect of altitude in the introduced range ($F_{1,54} = 12.27$, $P < 0.001$; data not shown) and non-significant effect in the native range ($F_{1,49} < 0.001$, $P > 0.97$; data not shown) were unaltered by the inclusion of these covariates.

DISCUSSION

General patterns of trait variation with altitude

All of our study species showed clear and similar responses to altitude in both the introduced and native ranges. Decreasing plant size and flower number with altitude is commonly

Table 4. Mixed-effects model (residual maximum-likelihood method) summaries for the effect of altitude and region on (log) capitulum number and seed size, shown for each of eight Asteraceae forbs separately.

	C. arvanse		***C. vulgare***		***C. intybus***		***L. serriola***	
Source	**df**	***F***	**df**	***F***	**df**	***F***	**df**	***F***
(Log) capitulum number								
Region (R)	16	10.41 **	20	2.36	15	5.29 *	15	21.94 ***
Altitude (A)	16	1.96	20	7.17 *	15	22.26 ***	15	16.86 ***
A x R	16	0.25	20	<0.01	15	7.93 *	15	1.83
Seed size								
Ontogeny	147	0.21	130	1.85	-	-	169	19.88 ***
Region (R)	15	0.99	20	0.27	14	0.26	16	0.51
Altitude (A)	15	8.19 *	20	4.83 *	14	0.09	16	19.21 ***
A x R	15	3.57	20	0.43	14	0.35	16	6.69 *

	C. canadensis		***E. annuus***		***M. discoidea***		***Solidago***	
Source	**df**	***F***	**df**	***F***	**df**	***F***	**df**	***F***
(Log) capitulum number								
Region (R)	17	0.17	18	29.28 ***	18	0.79	17	40.65 ***
Altitude (A)	17	8.98 **	18	23.67 ***	18	5.78	17	11.79 **
A x R	17	8.05 *	18	6.23 *	18	0.06	17	0.03
Seed size								
Ontogeny	172	8.32 **	76	4.40 *	159	25.08 ***	92	0.96
Region (R)	17	0.83	14	10.06 **	17	0.11	11	13.91 **
Altitude (A)	17	1.93	14	6.04 *	17	4.62 *	11	1.44
A x R	17	1.66	14	1.87	17	0.01	11	0.80

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. df, denominator degrees of freedom.

observed (e.g. Willis and Hulme 2002, Körner 2003, Baret et al. 2004) and in non-alpine species such as those we studied might be explained as a response to harsher growing conditions and a shorter season at high altitude. The observed variation in seed size with altitude, however, is not so easily explained, and both increases and decreases of seed size in response to altitude have been reported in other studies (Baker 1972, Totland and Birks 1996, Vera 1997, Blionis and Vokou 2002, Murray et al. 2003, Willis and Hulme 2004, Pluess et al. 2005).

Several authors have interpreted clinal changes in seed size as plastic responses to resource limitation (e.g. shorter growing season at high altitude/latitude; Baker 1972, Totland and Birks 1996, Moles and Westoby 2003, Murray et al. 2003) or to differences in heat sum (Willis and Hulme 2004). This interpretation is consistent with those studies that attribute the responses of alien invasive plants along altitudinal gradients to phenotypic plasticity (e.g. Williams et al. 1995, Parker et al. 2003, Baret et al. 2004). Plastic increases in seed size might also result from a "top-down" regulation of seed size due to resource partitioning (Obeso 2004, Weiner 2004). Because plant height scales isometrically with the *log* of capitulum number, and plants are smaller at higher altitude, high-altitude plants have relatively fewer capitula per unit plant size. Consequently, plants at high altitude should have relatively more resources to allocate to seeds within capitula. In contrast, other studies have put forward an adaptive explanation for differences in seed size, noting that seed size - although it can vary considerably among individuals of the same species - is a rather constrained trait evolutionarily (Murray et al. 2003, Pluess et al. 2005). Possible selective advantages of larger seeds at higher altitudes could result from their higher establishment success or greater resistance of seedlings to harsh climatic conditions (Harper 1977, Winn 1988, Vera 1997, Moles and Westoby 2004).

Previous authors (Becker et al. 2005) have hypothesised that the general decline in numbers of alien species with increasing altitude might be due to a lack of adaptation of invading populations to conditions along altitudinal gradients. If this were the case, we would expect to find this reflected in differences in patterns of trait variation along altitudinal gradients in the native and introduced ranges of species, especially in traits associated with fitness. For example, poorly adapted populations might be expected to have fewer capitula (as a proxy for reproductive output), and show a sharper decline in capitulum number with altitude. However, overall we found no consistent differences between native and introduced populations of species in patterns of variation in the traits measured (stem height, capitulum

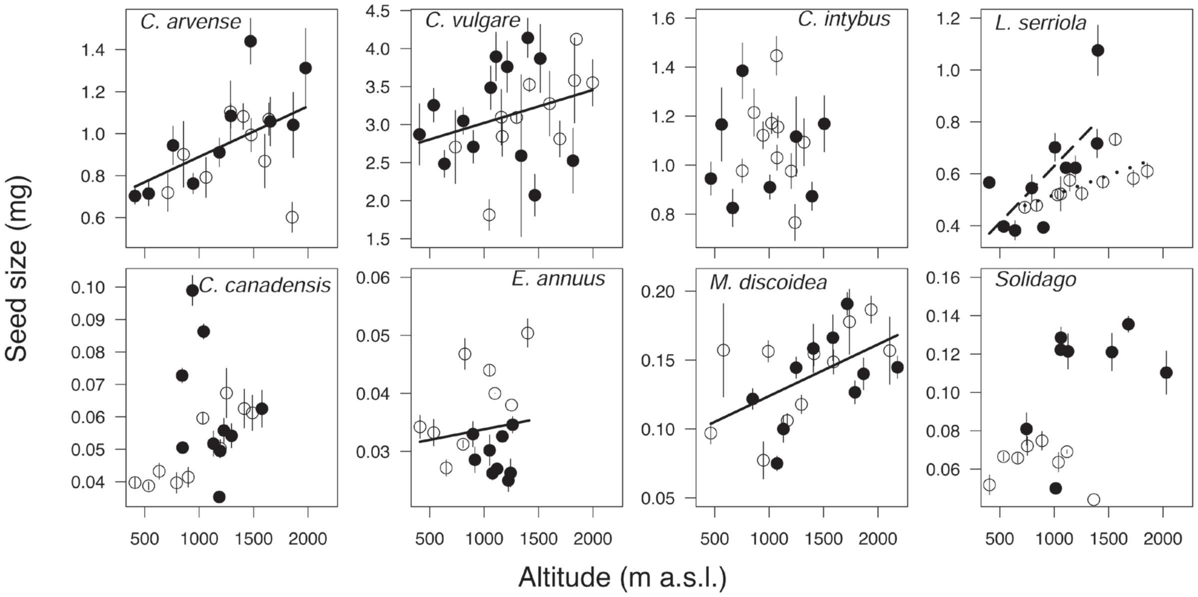


Fig. 4. Relationship between seed size and altitude in the native (filled circles) and introduced (open circles) ranges. Solid regression lines are fitted for a significant main effect of altitude on seed size ($P < 0.05$; see Table 4). Where altitude interacted significantly with species status, a dashed line is fitted for the relationship in the native range, and dotted line for that in the introduced range. No line is fitted for non-significant effects. The top four species in the panel are native to Europe and the bottom four native to North America. Data are population means with standard errors.

number, seed size), and no evidence that introduced populations suffer lower fitness or differ in their responses to high altitude conditions.

Furthermore, the species reached similar maximum altitudes in both systems (Chapter 1), even though the populations in the introduced range are rather recent (Table 1). Taken together, and contrary to our expectations, these observations suggest that the species respond to environmental variation in a similar way in both ranges. This implies either that populations in the introduced range exhibit considerable phenotypic plasticity, or that local adaptation has been very rapid (Lacey 1988, Weber and Schmid 1998, Murray et al. 2003, Cox 2004, Maron et al. 2004). Either way, the need to generate the necessary variation in the new range does not appear to have limited the spread of these species along altitudinal gradients.

Differential responses in allocation to capitula between native and introduced plants

Although plants generally responded in the same way to altitude in both native and introduced ranges, we found that plants in the new range differed in their patterns of resource allocation to capitula. The general increase in seed size with altitude, without a corresponding increase in capitulum seed mass, is consistent with there being a trade-off between seed size and number within capitula in the native range (Harper 1977, Venable and Brown 1988, Eriksson and Jakobsson 1999). Several possible functional links could exist between these two traits (assuming of course that they are genetically based and determined by different sets of genes), such that the optimal number of seeds per capitulum varies with seed size. For example, the combination of shorter stature and larger seeds at higher altitudes will have a strong negative effect on dispersal potential, since seed size affects the terminal velocity of a falling seed (Morse and Schmitt 1985, Tackenberg et al. 2003) while plant height affects the probability of a falling seed being dispersed by thermal uplifts (Sheldon and Burrows 1973, Tackenberg et al. 2003). A trade-off with seed number might thus prevent overcrowding within capitula which could interfere with dispersal (Sheldon and Burrows 1973), or large seeds might require a disproportionately large resource investment to the pappus to ensure dispersal (Morse and Schmitt 1985, Sakai et al. 1998, Eriksson and Jakobsson 1999).

In the introduced range, increasing seed size with altitude can be explained by the corresponding increase in capitulum seed mass. This indicates either that mechanisms regulating resource allocation to capitula have broken down in the new range, or that strategies for achieving increases in seed size have changed. For example, there might have been strong selection for increasing seed size with altitude in the new range, perhaps due to increased seedling survival and establishment, without a concomitant adjustment of seed number. This could be due to a weaker selection pressure operating on seed number than size, a lack of genetic variation in seed number, or complex epigenetic effects which mean that several generations have to go by before a new adaptive landscape is reached (Pigliucci and Murren 2003). Increasing resource allocation to capitula with altitude might thus be necessary to achieve adaptive increases in seed size.

Alternatively, increasing capitulum seed mass might be a mechanism to increase seed size via phenotypic plasticity (see above). Phenotypic plasticity can be very important for the establishment and spread of alien plants into a new area (Richards et al. 2006). Indeed, the pattern we have observed could be an example of genetic assimilation, the process by which a plastic response is turned into a genetically fixed response by selection under new environmental conditions (Pigliucci and Murren 2003, Richards et al. 2006). In this way, phenotypic plasticity in the introduced range might act as a "bridge" between different adaptive peaks. In the longer term, local adaptation might supercede these plastic responses by "fine-tuning" the match between genotype and environment to converge on patterns of adaptation observed in the native range (Dietz and Edwards 2006). Common garden experiments along altitudinal gradients, using plants of high and low origin from the native and introduced ranges, could test the basis of altitudinal variation in these traits. In particular these would demonstrate whether variation is genetically determined in both ranges, with selection pressures operating differently in each range, or due to phenotypic plasticity (in one or both ranges).

Variation among regions

The generally poorer performance of plants in the Wallowas, in terms of their steeper decline in stem height with altitude and lower capitulum number, illustrates the need to allow for region-specific effects when investigating the growth responses of alien plants along environmental gradients. Several studies have attempted to explain the invasive behaviour of alien plants by comparing their performance in parts of the native and introduced ranges (e.g. Vilà et al. 2003, Erfmeier and Bruelheide 2004, Jakobs et al. 2004). These field studies typically find that plant performance is enhanced in the introduced range (Bossdorf et al. 2005). If we had taken this approach using only the North American species, we would also have observed a general enhancement of performance in the new range. By contrast, if we had studied only the four European species, we would have observed that plant performance was generally poorer in the introduced range. Taking these observations independently, we might have concluded that some aspect of the process of introduction/invasion (e.g. enemy release, lack of adaptation to new conditions) is responsible for changes in performance (either improved or poorer) in the new range. However, our results indicate that plant performance is in general not dependent on introduction status, but rather on region-specific factors such as apparently small differences in climate or land use. For example, the poorer performance of plants in the Wallowas might be explained by drier conditions during the growing season, or the presence of relatively nutrient rich anthropogenic habitats along the altitudinal gradient in the Valais that ameliorate costs to plant performance. The importance of region-specific effects indicates that causal interpretations of changes in plant performance between native and introduced ranges might not be possible without a fully reciprocal approach.

CONCLUSIONS

Traits such as plant height and seed size have been recognised as very important functionally, and representative of different plant strategies (Westoby 1998). We observed a generally strong similarity in the altitudinal patterns of trait variation in both native and introduced populations of our study species, suggesting a convergence in strategies for coping with environmental variation. This consistency between ranges is intriguing and could reflect the relative conservatism of ecological niches (Prinzing et al. 2001, Martinez-Meyer and Peterson 2006), despite relocation to a new area with a potentially very different suite of selection pressures. That this consistency was present in two reciprocal study regions that clearly differed in region-specific effects on plant growth supports this interpretation. Still, we found evidence that the underlying internal mechanisms regulating potentially adaptive traits such as seed size might vary between ranges. Assuming that in the native range plants are more closely adapted to their environment (i.e. have developed the most cost-effective mechanisms to regulate fitness-related traits), this implies that ongoing adaptation to "fine-tune" these mechanisms in the introduced range could lead to greater invasion potential of the species in the future.

ACKNOWLEDGMENTS

Many thanks are due to Sabrina Schmid, Bridgett Naylor and Jane and Jesse Alexander for assistance in the field, and to Sabine Guesewell for statistical advice during preparation of the manuscript. This work was supported by a grant of the Swiss National Science Foundation to HD.

LITERATURE CITED

Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. Ecology **53**:997-1010.

Baker, H. G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics **5**:1-24.

Baret, S., S. Maurice, T. Le Bourgeois, and D. Strasberg. 2004. Altitudinal variation in fertility and vegetative growth in the invasive plant *Rubus alceifolius* (Rosaceae), on Réunion island. Plant Ecology **172**:265-273.

Becker, T., H. Dietz, R. Billeter, H. Buschmann, and P. J. Edwards. 2005. Altitudinal distribution of alien plant species in the Swiss Alps. Perspectives in Plant Ecology, Evolution and Systematics **7**:173-183.

Blionis, G. J., and D. Vokou. 2002. Structural and functional divergence of *Campanula spatulata* subspecies on Mt Olympus (Greece). Plant Systematics and Evolution **232**:89-105.

Bossdorf, O., H. Auge, L. Lafuma, W. E. Rogers, E. Siemann, and D. Prati. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia **144**:1-11.

Cox, G. W. 2004. Alien Species and Evolution. Island Press, Washington.

Daehler, C. C. 2005. Upper-montane plant invasions in the Hawaiian islands: Patterns and opportunities. Perspectives in Plant Ecology, Evolution and Systematics **7**:203-216.

Dietz, H., and P. J. Edwards. 2006. Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology **87**:1359-1367.

Dyrness, C. T. 1975. Grass-legume mixtures for erosion control along forest roads in western Oregon. Journal of Soil and Water Conservation **30**:169-173.

Erfmeier, A., and H. Bruelheide. 2004. Comparison of native and invasive *Rhododendron ponticum* populations: Growth, reproduction and morphology under field conditions. Flora **199**:120-133.

Eriksson, O., and A. Jakobsson. 1999. Recruitment trade-offs and the evolution of dispersal mechanisms in plants. Evolutionary Ecology **13**:411-423.

Fitzpatrick, M. C., J. F. Weltzin, N. J. Sanders, and R. R. Dunn. 2007. The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? Global Ecology and Biogeography **16**:24-33.

Glenz, C., A. Massolo, D. Kuonen, and R. Schlaepfer. 2001. A wolf habitat suitability prediection study in Valais (Switzerland). Landscape and Urban Planning **55**:55-65.

Hallet, S. G. 2006. Dislocation from coevolved relationships: a unifying theory for plant invasion and naturalization. Weed Science **54**:282-290.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, London.

Hegi, G. 1979. Illustrierte Flora von Mitteleuropa. Paul Parey, Berlin.

Hess, H. E., E. Landolt, and R. Hirzel. 1972. Flora der Schweiz und angrenzender Gebiete. Birkhäuser Verlag, Basel.

Hierro, J. L., J. L. Maron, and R. M. Callaway. 2005. A biogeographical appraoch to plant invasions: the importance of studying exotics in their introduced *and* native range. Journal of Ecology **93**:5-15.

Jakobs, G., E. Weber, and P. J. Edwards. 2004. Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. Diversity and Distributions **10**:11-19.

Körner, C. 2003. Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. 2nd edition. Springer, Berlin.

Lacey, E. P. 1988. Latitudinal variation in reproductive timing of a short-lived monocarp, *Daucus carota* (Apiaceae). Ecology **69**:220-232.

Landolt, E., and K. M. Urbanska. 2003. Our Alpine Flora. SAC Publications, Frutigen.

Legendre, P., and L. Legendre. 1998. Numerical Ecology. Elsevier, Amsterdam.

Lloret, F., F. Médail, G. Brundu, I. Camarda, E. Moragues, J. Rita, P. Lambdon, and P. E. Hulme. 2005. Species attributes and invasion success by alien plants on Mediterranean islands. Jounral of Ecology **93**:512-520.

Maron, J. L., M. Vila, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004. Rapid evolution of an invasive plant. Ecological Monographs **74**:261-280.

Martinez-Meyer, E., and A. T. Peterson. 2006. Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. Journal of Biogeography **33**:1779-1789.

Moles, A., and M. Westoby. 2003. Latitude, seed predation and seed mass. Journal of Biogeography **30**:105-128.

Moles, A., and M. Westoby. 2004. Seedling survival and seed size: a synthesis of the literature. Journal of Ecology **92**:372-383.

Morse, D. H., and J. Schmitt. 1985. Propagule size, dispersal ability and seedling performance in *Asclepias syriaca*. Oecologia **67**:372-379.

Murray, B. R., A. H. D. Brown, and J. P. Grace. 2003. Geographic gradients in seed size among and within perennial Australian *Glycine* species. Australian Journal of Botany **51**:47-56.

Obeso, J. R. 2004. A hierarchical perspective in allocation to reproduction from whole plant to fruit and seed level. Perspectives in Plant Ecology, Evolution and Systematics **6**:217-225.

Parker, I. M., J. Rodriguez, and M. E. Loik. 2003. An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. Conservation Biology **17**:59-72.

Parks, C. G., S. R. Radosevich, B. A. Endress, B. J. Naylor, D. Anzinger, L. J. Rew, B. D. Maxwell, and K. A. Dwire. 2005. Natural and land-use history of the Northwest mountain ecoregions (USA) in relation to patterns of plant invasions. Perspectives in Plant Ecology, Evolution and Systematics **7**:137-158.

Peterson, A. T. 2003. Predicting the geography of species' invasions via ecological niche modelling. The Quarterly Review of Biology **78**:419-433.

Pigliucci, M., and C. J. Murren. 2003. Genetic assimilation and a possible evolutionary paradox: Can macroevolution sometimes be so fast as to pass us by? Evolution **57**:1455-1464.

Pluess, A. R., W. Schütz, and J. Stöcklin. 2005. Seed weight increases with altitude in the Swiss Alps between related species but not among populations of individual species. Oecologia **144**:55-61.

Pohs, K. 2000. The Wallowa Mountains: A Natural History Guide. Northwest Mountain Works, Portland.

Prinzing, A., W. Durka, S. Klotz, and R. Brandl. 2001. The niche of higher plants: Evidence for phylogenetic conservatism. Proceedings of the royal Society of London B **268**:2383-2389.

Rebetez, M., and M. Dobbertin. 2004. Climate change may already threaten Scots pine stands in the Swiss Alps. Theoretical and Applied Climatology **79**:1-9.

Richards, C. L., O. Bossdorf, N. Z. Muth, J. Gurevitch, and M. Pigliucci. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters **9**:981-993.

Sakai, S., K. Kikuzawa, and K. Umeki. 1998. Evolutionary stable resource allocation for production of wind-dispersed seeds. Evolutionary Ecology **12**:477-485.

Semple, J. C., and R. E. Cook. 2006. Asteraceae. Pages 151-157 Flora of North America Editorial Committee, eds 1993+. Flora of North America North of Mexico. 12+ vols., New York and Oxford.

Sexton, J. P., J. K. McKay, and A. Sala. 2002. Plasticity and genetic diversity may allow saltceder to invade cold climates in North America. Ecological Applications **12**:1652-1660.

Sheldon, J. C., and F. M. Burrows. 1973. The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. New Phytologist **72**:665-675.

Tackenberg, O., P. Poschlod, and S. Bonn. 2003. Assessment of wind dispersal potential in plant species.

Ecological Monographs **73**:191-205.

Totland, Ø., and H. J. B. Birks. 1996. Factors influencing inter-population variation in *Ranunculus acris* seed production in an alpine area of southwestern Norway. Ecography **19**:269-278.

Venable, D. L., and J. S. Brown. 1988. The selective interactions of dispersal, dormancy and seed size as adaptations for reducing risk in variable environments. The American Naturalist **131**:360-384.

Vera, M. L. 1997. Effects of altitude and seed size on germination and seedling survival of heathland plants in north Spain. Plant Ecology **133**:101-106.

Vilà, M., A. Gomez, and J. L. Maron. 2003. Are alien plants more competitive than their native conspecifics? A test using *Hypericum perforatum* L. Oecologia **137**:211-215.

Weber, E., and B. Schmid. 1998. Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. American Journal of Botany **85**:1110-1121.

Weiner, J. 2004. Allocation, plasticity and allometry in plants. Perspectives in Plant Ecology, Evolution and Systematics **6**:207-215.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil **199**:213-227.

Williams, D. G., R. N. Mack, and R. A. Black. 1995. Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. Ecology **76**:1569-1580.

Willis, S. G., and P. E. Hulme. 2002. Does temperature limit the invasion of *Impatiens glandulifera* and *Heracleum mantegazzianum* in the UK? Functional Ecology **16**:530-539.

Willis, S. G., and P. E. Hulme. 2004. Environmental severity and variation in the reproductive traits of *Impatiens glandulifera*. Functional Ecology **18**:887-898.

Winn, A. A. 1988. Ecological and evolutionary consequences of seed size in *Prunella vulgaris*. Ecology **69**:1537-1544.

Appendix 1. Mixed-effects model (residual maximum-likelihood method) summaries for the effect of altitude and region on stem height and capitulum seed mass, shown for each of eight Asteraceae forbs separately. Only denominator degrees of freedom (df) are given, since all numerator df's are 1.

	C. arvanse		*C. vulgare*		*C. intybus*		*L. serriola*		*C. canadensis*		*E. annuus*		*M. discoidea*		*Solidago*	
Source	**df**	***F***	**df**	***F***	**df**	***F***	**df**	***F***	**df**	***F***	**df**	***F***	**df**	***F***	**df**	***F***
Stem height																
Region (R)	15	11.56 **	20	0.24	15	0.09	16	3.36	17	0.45	18	6.32 *	18	2.76	17	79.85 ***
Altitude (A)	15	0.68	20	16.64 ***	15	0.33	16	25.23 ***	17	7.88 *	18	<0.01	18	<0.01	17	39.81 ***
A x R	15	35.93 ***	20	<0.01	15	0.09	16	9.34 **	17	6.81 *	18	3.55	18	0.13	17	4.20
Capitulum seed mass																
Region (R)	13	3.54	18	0.10	14	6.70 *	16	3.72	17	1.41	7	8.30 *	17	4.10	11	2.68
Altitude (A)	13	0.08	18	0.47	14	0.38	16	0.68	17	0.19	7	7.80 *	17	16.12 ***	11	0.37
A x R	13	1.24	18	<0.01	14	0.25	16	0.06	17	0.04	7	1.53	17	0.09	11	1.16

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Appendix 2. Mixed-effects model (residual maximum-likelihood method) summaries for traits measured in eight Asteraceae forbs in their native and introduced ranges. These are the same data as in Table 3, but without the three-way interaction of A x R x S and with the inclusion of additional covariables (see text). Numerator degrees of freedom (df) are 1 for all variables except population size (df = 2).

	Stem height			**(Log) capitulum number**			**Seed size**			**Capitulum seed mass**		
Source	**df**	***F***	***P***	**df**	***F***	***P***	**df**	***F***	***P***	**df**	***F***	***P***
Site type	129	13.77	<0.001	129	16.81	<0.001	119	0.11	0.743	107	0.49	0.487
Population size	129	2.25	0.109	129	4.21	0.017	119	4.23	0.017	107	4.07	0.020
Ontogeny	1287	0.71	0.400	1292	0.58	0.445	958	26.33	<0.001	752	44.25	<0.001
Region (R)	5	4.07	0.100	5	9.17	0.029	5	0.21	0.664	5	0.80	0.413
Status (S)	5	0.58	0.482	5	0.40	0.557	5	0.40	0.553	5	3.47	0.121
Altitude (A)	129	29.13	<0.001	129	35.67	<0.001	119	33.34	<0.001	107	5.41	0.022
A x R	129	<0.01	0.976	129	0.15	0.699	119	0.07	0.793	107	3.16	0.078
A x S	129	31.77	<0.001	129	4.36	0.039	119	1.26	0.264	107	0.04	0.851

Chapter 3

Changes in genetic structure and variation of two Asteraceae forbs invading into mountainous regions

Jake M. Alexander, Myriam Poll, Hansjörg Dietz, Peter J. Edwards

Institute of Integrative Biology, ETH Zürich, Universitätsstrasse 16, 8092 Zürich, Switzerland

ABSTRACT

Changes in the levels and partitioning of genetic variation that accompany the introduction of an alien species can have profound implications for its spread and success in a new range. However, the extent to which these changes relate to the progression of invasions along environmental gradients has rarely been studied. Using a reciprocal approach, we investigate how patterns of variation and population structure at microsatellite loci of two species, *Lactuca serriola* and *Solidago canadensis*, differ in mountain areas of their native and introduced ranges in North America and Europe. *S. canadensis* appears to have experienced a strong bottleneck on introduction to Europe, but this has apparently not prevented it from colonising a wide altitudinal range. By contrast, *L. serriola* is more variable in the introduced area in North America and also occurs over a greater altitudinal range in this region than in the native area. We conclude that the ecological amplitude of alien species may be enhanced by multiple introductions to the new range, and that even genetically depauperate introduced populations can colonise the full ecological range along environmental gradients which they occupy in the native range.

Keywords: Alien invasive plant, altitudinal gradient, elevation, comparative approach, microsatellite, genetic variation, bottleneck.

INTRODUCTION

The importance of evolutionary processes during invasions by alien species is becoming increasingly recognised (Ellstrand and Schierenbeck 2000, Lee 2002). Typically, introduced populations are expected to pass through genetic bottlenecks, with allelic diversity being lost through both founder effects and drift. The severity of these bottlenecks depends on the distribution of genetic variation within the native range, the breeding system of the species and its introduction history (i.e. the quantity and sources of introduced propagules; Novak and Mack 2005, Taylor and Keller 2007). Most genetic variation in out-crossing species is usually partitioned within populations, so that few introductions are needed to sample a genetically diverse inoculum. By contrast, most variation of highly inbreeding species is partitioned between populations and so these are more likely to experience the effects of a genetic bottleneck. However, comparisons of neutral genetic variation between introduced and native populations have revealed that many species do not experience severe bottlenecks on introduction to a new range (Bossdorf et al. 2005, Novak and Mack 2005). Furthermore, admixture of previously isolated lineages in the native range through multiple introductions can generate increased diversity in the new range, potentially leading to the evolution of “invasiveness” (Ellstrand and Schierenbeck 2000, Kolbe et al. 2004). And even when the loss of genetic diversity is considerable, this may not prevent an alien species from spreading; indeed, the fixation of highly successful “invasive genotypes” might explain the success of some alien species which are virtually devoid of genetic variation in their new ranges (Amsellem et al. 2000, Hollingsworth and Bailey 2000).

Because the amount of genetic variation within a population determines its ability to respond to selection (Futuyma 1998), a lack of variation could restrict the spread of alien species along environmental gradients, especially given that variation is expected to be eroded by consecutive founder events in small and isolated peripheral populations at the invasion front (Frankham 1996, Chauvet et al. 2004). It has been suggested that the failure of some species to extend their ecological range in a new area might be due to insufficient genetic variation (cf. Hoffmann and Blows 1994, Lee 2002, Dietz and Edwards 2006). However, many species appear to have similar ecological amplitudes in both the native and introduced ranges, suggesting that when species are introduced into new areas their niches are commonly conserved (Wiens and Graham 2005). For example, in previous studies we have shown that the altitudinal limits and clinal patterns of trait variation along altitudinal gradients of eight Asteraceae species are remarkably similar between their native and introduced ranges, and that these patterns have emerged within c. 100 years of their introduction (Chapters 1 and 2). Thus the link between allelic diversity and traits determining the ecological amplitude of invading populations along environmental gradients might not be strong (Reed and Frankham 2001).

Relatively few studies have directly compared population genetic structure (i.e. the partitioning of genetic variance among populations) and variability of alien plants between their native and introduced ranges (see Bossdorf et al. 2005 for a recent review), and we are aware of none which relate these to the spread of alien species along environmental gradients. Altitudinal gradients are particularly useful in this regard, because factors that might limit or delay an invasion, such as climatic conditions and anthropogenic disturbance/propagule pressure, vary over small geographic scales (Arévalo et al. 2005, Parks et al. 2005, Dietz and Edwards 2006). Variation in population structure along altitudinal gradients can result from temporal/physical barriers to gene flow which commonly exist along the gradient. For example, the altitudinal differentiation among populations of *Primula farinosa* described by Reisch et al. (2005) was attributed to barriers imposed by forests below the tree-line and delayed phenology at higher altitudes. Such structure might promote, or result from, adaptation to local site conditions along the gradient (Aradhya et al. 1993, Semagn et al. 2001). However, population structure is typically reduced in the introduced range of invading species (Bossdorf et al. 2005). Thus, insights into the extent to which genetic variation and structure affect the progression of an invasion can be gained by comparing populations along altitudinal gradients in the native and introduced ranges (Bossdorf et al. 2005, Hierro et al. 2005).

Here, we report on levels of genetic variation at microsatellite loci and population structure of two Asteraceae species, *Lactuca serriola* and *Solidago canadensis*, in mountainous areas in their native and introduced ranges. Our aim was to understand how an altered pattern of genetic variation in the introduced range might affect the ability of a species to invade along an altitudinal gradient. We hypothesised that (1) overall genetic variation would be lower in introduced populations due to bottlenecks exacerbated by isolation and restricted gene flow within mountain systems. We also expected that (2) population structure would be weaker in the introduced area, particularly in relation to altitude, and that (3) genetic variation would decrease with altitude due to consecutive founder events at the upper range margin. Additionally, we asked (4) to what extent these patterns are affected by differences in the breeding system between the two species. The potential impact of our findings on plant invasions into mountains is discussed.

METHODS

Study species

Solidago canadensis L. (Asteraceae; Canada goldenrod) is a perennial, diploid (2n = 18) forb, producing new stems up to c. 120 cm tall each year from underground rhizomes. It is an obligate out-crosser, flowering between the end of August and October, and can produce in the order of 20,000 achenes per ramet (Dong et al. 2006). Achenes are small (c. 0.1 mg), bear a pappus and are readily dispersed by wind and other agents. It also spreads clonally from rhizomes, and forms dense stands which are able to exclude competing species. It is typical of old-field habitats, and in its introduced range it grows not only in disturbed ruderal areas but also invades semi-natural vegetation (Weber 1997).

In its native range in northeastern North America, *S. canadensis* is distributed from Virginia in the south to Ontario in the north and across the Great Plains to the west (Semple and Cook 2006). In Europe it is widely distributed from Ireland to Russia, and Scandinavia to northern Italy (Weber 1997), and is also invasive in China (Dong et al. 2006). The altitudinal distribution is constrained by the fact that only very few mountain peaks in its native range extend above 1200 m a.s.l. (highest point Mt. Washington 1917 m a.s.l.), although it probably occupies much of this altitudinal range (this study). It has been recorded up to 1530 m a.s.l. in the Swiss Alps (Chapter 1). *S. canadensis* was introduced to botanic gardens in Paris and London from either Maryland/Virginia or Canada before 1750 (Weber 1994). As an ornamental plant, it was probably introduced on a few occasions in the 18th century and then widely distributed to gardens throughout Europe (Weber 1994).

Lactuca serriola L. (Asteraceae; Prickly lettuce) is an annual, diploid (2n = 18) forb which flowers and sets seed between July and October. It is a species typical of ruderal plant communities, roadsides and sand dunes and populations tend to be rather transient (Lebeda et al. 2001, Hooftman et al. 2006). Plants grow up to c. 130 cm, producing many hundreds of yellow capitula, each bearing on average 16 wind-borne and highly dispersable achenes (Chapter 2). Pollination is usually autogamous although insect pollination and out-crossing has been observed (Hooftman et al. 2006).

Lactuca serriola is native to Eurasia but has been introduced extensively to many parts of the world including North America. It has also become more common in Europe in the last 50 years (Lebeda et al. 2001, Hooftman et al. 2006). It has probably been introduced many times to North America as a contaminant of seed crops (Forcella and Harvey 1988, Mack and Erneberg 2002), and is now present in all conterminous U.S. states and even on Hawaii. Settlers probably brought the species to northeast Oregon around the middle of the 19th century, and it spread into the Wallowa Mountains around the turn of the 20th century when mining became important in the region (Pohs 2000). In Europe it is most abundant below 600 m a.s.l. but has been observed up to 1560 m a.s.l. in the Valais (Swiss Alps; Lebeda et al. 2001 and references therein), though populations and plants above c. 800 m a.s.l. in Europe are usually small with limited seed set (Lebeda et al. 2001, Chapter 2). In the Wallowa Mountains plants have been found up to 1860 m a.s.l. (Chapter 1).

Sampling scheme

We sampled a total of 12 populations of *L. serriola* and 20 of *S. canadensis* from three temperate mountain areas during the summers of 2005 and 2006 (Table 1). Six native populations of *L. serriola* and 12 introduced populations of *S. canadensis* were sampled from canton Valais in the southern Swiss Alps (46°10′N, 7°20′E). A further six populations of *L. serriola* were sampled from part of its introduced range in the Wallowa Mountains in eastern Oregon, U.S.A. (45°15′N, 117°20′W). Both these regions experience similar continental climates (see Chapters 1 and 2 for a more detailed description). Eight populations of *S. canadensis* were collected from the Allegheny Mountains (39°00′N, 79°00′W), which constitute part of the Appalachian range, principally from West Virginia, U.S.A. (Fig. 1; Table 1). This area experiences a humid continental climate, with mean monthly temperatures in the mountains ranging from 3.5–16.5°C, and a mean monthly precipitation of 1035 mm (<http://www.sercc.com>).

Populations were selected to cover a broad range of altitude in each area. Where possible, pairs of high and low altitude populations were sampled that were geographically closer to each other than to other pairs of populations, although this design was not possible in the Valais due to the scarcity of suitable populations (Fig. 1). From each population, leaf material was collected from up to 30 individuals which were at least 2 m apart and dried on silica gel. Voucher specimens are lodged in the herbarium of the ETH Zurich.

Table 1. Locations and measures of genetic diversity of sampled populations: *N*, the number of sampled individuals; *A*, allelic richness; H_O, observed heterozygosity; H_T, gene diversity; F_{IS}, inbreeding coefficient; P_{GT}, the proportion of unique multilocus genotypes; *PA*, number of private alleles.

ID	†Location	Altitude (m a.s.l.)	*N*	*A*	H_O	H_T	F_{IS}		P_{GT}	*PA*
Solidago canadensis										
Sc1	Täsch, VS	1414	12	2.536	0.345	0.499	0.272		1.000	0
Sc2	Ayent, VS	1039	29	2.259	0.409	0.461	0.067		0.897	0
Sc3	Vex, VS	888	21	2.845	0.476	0.570	0.160		1.000	0
Sc4	Lax, VS	1046	10	2.606	0.357	0.567	0.241		1.000	0
Sc5	Obergesteln, VS	1365	8	2.229	0.375	0.454	0.152		1.000	0
Sc6	Goppenstein (1), VS	1117	30	2.615	0.367	0.503	0.250	*	1.000	0
Sc7	Goppenstein (2), VS	1240	15	2.747	0.400	0.559	0.233		1.000	0
Sc8	Sierre, VS	534	30	3.048	0.433	0.611	0.273	*	1.000	0
Sc9	Visp, VS	651	6	3.021	0.333	0.648	0.478	*	1.000	0
Sc10	Gamsen, VS	664	30	2.696	0.481	0.523	0.030		0.967	0
Sc11	Bex, VS	410	10	2.892	0.357	0.553	0.113		1.000	0
Sc12	Monthey, VS	405	24	2.443	0.393	0.497	0.130		1.000	0
Sc13	Mt. Davis, PA	824	25	3.418	0.463	0.653	0.266	*	1.000	1
Sc14	Dolly Sods, WV	1217	22	3.526	0.506	0.631	0.197	*	0.773	1
Sc15	Mt. Storm, WV	1007	29	2.992	0.448	0.582	0.207	*	1.000	2
Sc16	Spruce Knob, WV	1407	30	2.706	0.495	0.547	0.085		1.000	2
Sc17	Lonaconing, MD	465	23	3.519	0.528	0.628	0.133		1.000	4
Sc18	Smoke Hole, WV	336	26	3.328	0.363	0.636	0.391	*	1.000	1
Sc19	Greenland Gap, WV	382	24	3.081	0.458	0.588	0.214	*	1.000	0
Sc20	Riverton, WV	568	28	3.405	0.480	0.687	0.256	*	1.000	1
Lactuca serriola										
Ls1	Magas d'Arbaz, VS	1394	24	3.21	0.012	0.342	0.965	*	0.375	2
Ls2	Vissoie, VS	1195	24	2.60	0.000	0.488	1.000	*	0.167	0
Ls3	Naters, VS	1252	15	1.86	0.010	0.252	0.962	*	0.200	1
Ls4	Sierre, VS	534	24	4.23	0.024	0.608	0.961	*	0.542	0
Ls5	Gamsen, VS	664	24	3.68	0.042	0.403	0.897	*	0.375	2
Ls6	Monthey, VS	403	24	2.54	0.036	0.428	0.917	*	0.375	6
Ls7	Mt Harris loop, OR	1239	24	5.532	0.095	0.731	0.870	*	0.875	1
Ls8	Moss Springs road, OR	1641	23	4.646	0.056	0.670	0.917	*	0.739	2
Ls9	Fish Lake road, OR	1459	24	4.147	0.030	0.394	0.925	*	0.583	1
Ls10	Ladd Canyon road, OR	1000	24	5.666	0.101	0.724	0.860	*	1.000	4
Ls11	Fish Lake road, OR	834	24	4.390	0.036	0.642	0.944	*	0.708	1
Ls12	Mt Harris loop, OR	900	24	5.282	0.030	0.687	0.957	*	0.792	0

*Significant effect ($P < 0.001$). †Locality, State (U.S.A.)/Canton (Switzerland): VS, Valais; MD, Maryland; OR, Oregon; PA, Pennsylvannia; WV, West Virginia.

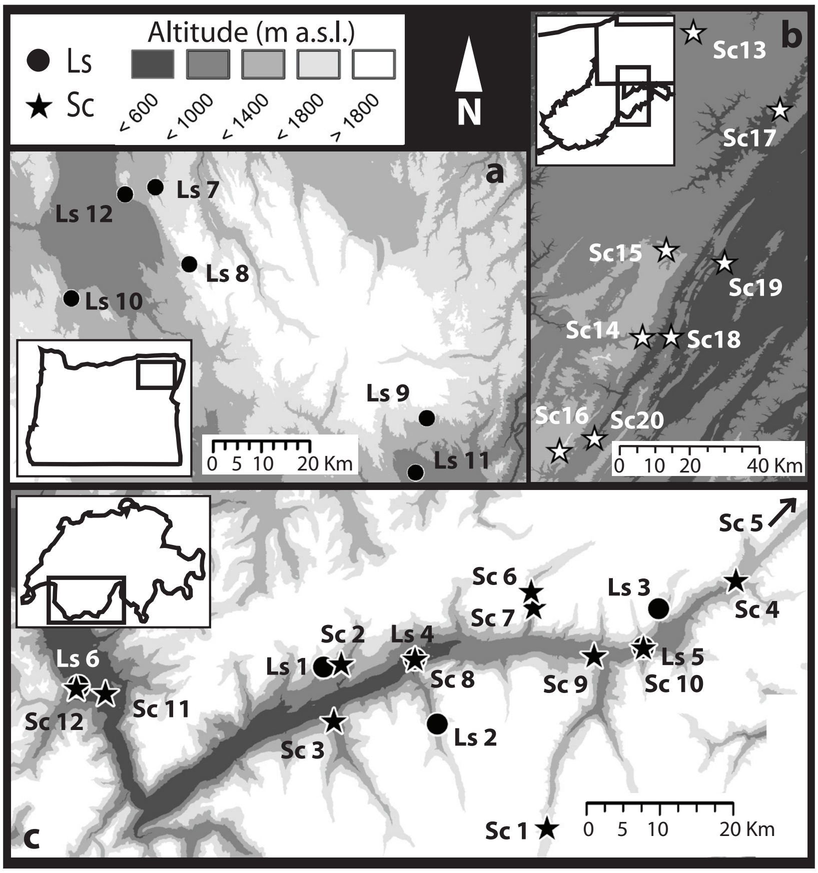


Fig. 1. Topographic maps of the study areas, with locations of the sampled populations; a, Wallowa Mountains, Oregon, U.S.A.; b, Allegheny Mountains, West Virginia, U.S.A.; c, Canton Valais, Switzerland (reproduced by permission of swisstopo (BA071648)). Note population Sc5 is located outside the range of the map.

Microsatellite analysis

DNA of *L. serriola* was extracted using a modified CTAB procedure (Hoelzel 1998), and of *S. canadensis* using a silica gel technique (Elphinstone et al. 2003). Microsatellite analyses of *L. serriola* were performed for seven loci (A001, A004, B101, B104, D106, D108, E011) using primers designed for *L. sativa* by van de Wiel et al. (1999). Forward primers were fluorescently labelled with either NED, FAM or HEX. Polymerase chain reaction (PCR) was performed in a total volume of 10 µL with 5 µL template DNA (1 ng.µL^{-3}), 1 x reaction buffer, 1.5–3.0 mM $MgCl_2$, 0.2 mM of each dNTP, 0.4 µM of each primer and 0.5U Amplitaq Gold™ DNA polymerase (Applied Biosystems). PCR amplifications consisted of an initial denaturation at 95°C for 9 minutes followed by 30–35 cycles of 95°C, annealing temperatures of 55–60°C depending on the locus and 72°C for 30 seconds each, with a final elongation at 72°C for 5 minutes.

Analyses of *S. canadensis* were performed for seven loci (SS1B, SS4F, SS4G, SS19C, SS19D, SS20E, SS24F) using primers developed for *S. sempervirens* (Wieczorek and Geber 2002). PCR conditions were as above, except that each reaction contained 0.3 μM of each labelled primer, 1.5 mM $MgCl_2$ and 2 μL of template DNA (5 $ng.\mu L^{-3}$). PCR amplification was performed with an initial amplification of 15 minutes at 95°C followed by 30 cycles of annealing temperatures of 53–60°C, 72°C and 95°C for 30 seconds, with a final annealing step for 1 minute and 72°C for 30 minutes.

PCR products were denatured at 92°C for 3 minutes and separated on an ABI PRISM 3130xl Genetic Analyser (Applied Biosystems) with GeneScan ROX or LIZ as the internal size standard. Individuals were genotyped using the GeneMapper v.3.7 software (Applied Biosystems). Cases where loci failed to amplify after three attempts were scored as null alleles. In total, amplification failed at at least one locus for 20% of *S. canadensis* and 15% of *L. serriola* individuals. Null alleles were detected at all 14 loci.

Statistical analysis

Analyses of clonal species are usually conducted at both the ramet and genet levels because sampling clones multiple times can bias the representation of alleles in a population (Jump et al. 2003). However, because duplicate multilocus genotypes of *S. canadensis* were extremely rare (4% of all sampled individuals; cf. Dong et al. 2006), only ramet-level analyses are reported.

Genetic variation within populations, measured as Nei's (1987) gene diversity (H_T) and allelic richness (A), as well as the inbreeding coefficient (F_{IS}), were calculated using FSTAT v2.9.3 (Goudet 2001). The calculation of allelic richness controls for differences in sample sizes by using rarefaction (El Mousadik and Petit 1996). Thus allelic richness was adjusted to a minimum population size of four individuals for *S. canadensis* and 15 individuals for *L. serriola*. Observed heterozygosity, private alleles within populations and allele frequencies were determined using GenAlEx v6 (Peakall and Smouse 2006). Multiple regression models were fitted in R (R Development Core Team, 2006) to investigate how patterns of genetic diversity (A, H_T, proportion of unique multilocus genotypes) and structure (H_O, F_{IS}) of populations changed with altitude in each range.

Hierarchical partitioning of genetic variation within and between populations and ranges was assessed using analysis of molecular variance (AMOVA; Excoffier et al. 1992) in ARLEQUIN v3.01 (Excoffier et al. 2006), with significance tested by 1023 permutations of individuals within populations/regions, and populations within regions (Excoffier et al. 2006). Within each region, additional analyses were performed to investigate the partitioning of genetic variation between groups of high-/low-altitude populations (threshold 1000 m a.s.l., or 800 m a.s.l. for *S. canadensis*) or pairs of geographically close high/low altitude populations. This design was not possible in the Valais, where populations east and west of Sierre (central Valais) were grouped together, with the *L. serriola* population Ls6 in Martigny (western Valais) forming a separate group.

The significance of deviations from Hardy-Weinberg equilibrium (HWE) were tested for each locus by permuting alleles among individuals within populations in FSTAT based on 1000 permutations and applying Bonferroni corrections for multiple comparisons (Goudet 2001). FSTAT was also used to test for significant genotypic disequilibrium between pairs of loci based on 2100 randomisations of alleles within loci after Bonferroni corrections.

The correlations between Nei's (1972) genetic distance (*D*) and (1) (log) geographic and (2) (log) altitudinal distances between pairs of populations were assessed with IBDWS v3.12 and tested using a Mantel test with 1000 permutations (Rousset 1997, Jensen et al. 2005). To

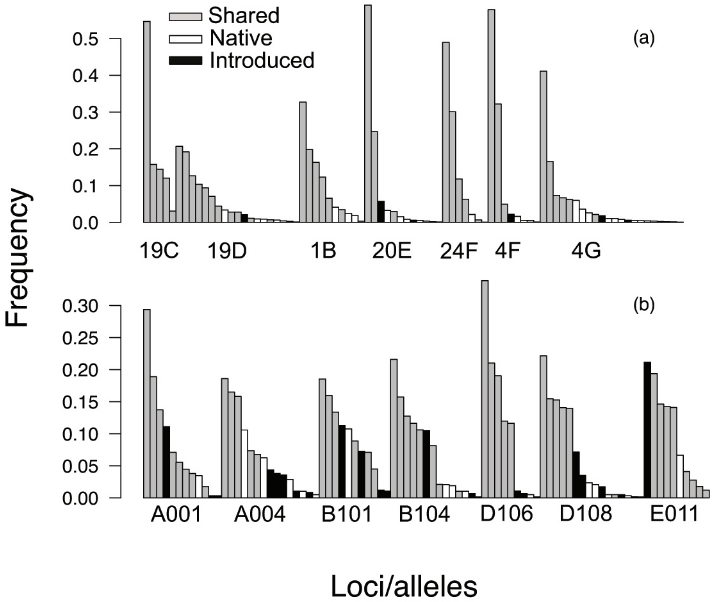


Fig. 2. Rank abundance plots of the 83 alleles at seven microsatellite loci in (a) *Solidago canadensis* and 87 alleles at seven loci in (b) *Lactuca serriola*, showing alleles shared between both areas, and those found only in native or introduced populations.

additionally investigate the structuring of populations in each region, cluster analysis was performed based on Nei's (1972) genetic distance between pairs of populations using the PHYLIP v3.66 package (Felsenstein 2006). 1000 bootstrap replicates of the allele frequency data were generated using SEQBOOT and distance matrices for each calculated using GENDIST. UPGMA unrooted tree topologies were created for all replicates using NEIGHBOUR, and the consensus tree drawn using CONSENSE.

RESULTS

Allelic diversity at the species level

In total we detected 83 alleles at seven loci (including seven null alleles; mean 11.9 per locus) in *S. canadensis*, 41 of which were present in both areas. Thirty-six alleles were found only in the native area (North America), whilst six were present only in the Valais (Fig. 2a). The shared alleles included the most common in both areas (mean frequencies 0.14 and 0.17

Table 2. Comparison of genetic diversity in native and introduced populations of *Solidago canadensis* and *Lactuca serriola*. See Table 1 for explanation of abbreviations. Statistically significant differences ($P < 0.05$) are indicated by bold-face type.

	Native range		**Introduced range**		**t-test**
	Mean	**SE**	**Mean**	**SE**	***P***
S. canadensis					
A	2.661	0.006	3.247	0.011	**0.000**
PA	NA	NA	NA	NA	NA
H_O	0.394	0.000	0.468	0.000	**0.004**
H_T	0.537	0.000	0.619	0.000	**0.003**
F_{IS}	0.200	0.001	0.219	0.001	0.712
P_{GT}	0.989	0.000	0.972	0.001	0.581
L. serriola					
A	3.020	0.123	4.944	0.067	**0.001**
PA	1.833	0.828	1.500	0.317	0.762
H_O	0.020	0.000	0.058	0.000	**0.030**
H_T	0.420	0.002	0.641	0.003	**0.011**
F_{IS}	0.950	0.000	0.912	0.000	0.114
P_{GT}	0.339	0.003	0.783	0.003	**0.000**

in the native/introduced areas respectively), and there was a strong correlation between the frequencies of these alleles in both areas ($r = 0.73$, df = 39, $P < 0.001$). There was a large variation in allele frequencies (range 0.001–0.591, mean, SD; 0.084, 0.136). From a total of 432 *S. canadensis* individuals we detected 423 unique multilocus genotypes, and 96% of the individuals that we analysed were genetically distinct using these markers. Three multilocus genotypes occurred twice, and one three times, in population Sc14, and two occurred one time each in populations Sc2 and Sc10. No multilocus genotype occurred in more than one population.

L. serriola showed a very different pattern. We recorded a total of 87 alleles at seven loci (including seven null alleles; mean 12.4 per locus), 46 of which were detected in both areas, 18 of which were found only in the Valais and 23 only in the Wallowa Mountains. The shared alleles were amongst the most common overall (mean frequencies 0.13 and 0.11 in the native/introduced ranges respectively; Fig 2b), although there was no correlation between the frequencies of these alleles between areas ($r = 0.03$, df = 44, $P > 0.8$). Furthermore, some alleles which were very common in one area (e.g. E011-288) were absent in the other (Fig. 2b). Allele frequencies varied less than for *S. canadensis* (range 0.002–0.339, mean, SD; 0.087, 0.079). From a total of 278 individuals, we detected 157 unique multilocus genotypes, 83.4% of which occurred only once. Only 47.1% of the individuals analysed were genetically distinct using these markers. Of the 26 multilocus genotypes which occurred more than once, some occurred up to 16 times (mean 5.7 times). Only two multilocus genotypes (one in the Valais, one in the Wallowas) were found to occur in two populations. More than twice as many multilocus genotypes were found in the Wallowas (111) than in the Valais (46).

Genetic diversity within populations

Genetic diversity of *S. canadensis*, in terms of both Nei's (1987) gene diversity (H_T) and allelic richness (A), was significantly greater within populations in the native area (Table 2). Observed heterozygosity (H_O) was also greater in the native area (Table 2). In multiple regression models, allelic richness and gene diversity both decreased significantly with altitude and were significantly greater in the native area, although the relationship between diversity and altitude did not differ between areas (non-significant interactions; Appendix 1, Fig. 3). Deviations from HWE (observed heterozygosity, F_{IS}) did not vary significantly with altitude (Appendix 1).

Populations of *L. serriola* were significantly more diverse (A, H_T) and contained a greater diversity of multilocus genotypes (P_{GT}) in the introduced area, and also had higher observed

Table 3. Results of the AMOVA (analysis of molecular variance) showing the distribution of genetic variation (% var.) among regions, populations and individuals. "SS", sums of squares; "Var. com.", variance components.

	S. canadensis					***L. serriola***				
Source	**df**	**SS**	**Var. com.**		**% var.**	**df**	**SS**	**Var. com.**		**% var.**
Both areas										
Among regions	1	82.9	0.158	***	6.2	1	102.3	0.172	**	5.5
Among pops within regions	18	235.7	0.258	***	10.2	10	538.4	1.124	***	35.7
Within populations	844	1795.2	2.127	***	83.7	544	1006.4	1.850	***	58.8
Total	863	2113.8	2.543			555	1647.1	3.147		
Native area										
Among populations	7	107.0	0.253	***	10.2	5	372.5	1.630	***	52.4
Within populations	406	907.9	2.236	***	89.9	264	390.3	1.479	***	47.6
Total	413	1014.9	2.489			269	762.8	3.108		
Introduced area										
Among populations	11	128.7	0.264	***	11.5	5	165.9	0.650	***	22.8
Within populations	438	887.3	2.026	***	88.5	280	616.1	2.200	***	77.2
Total	449	1016.0	2.289			285	782.0	2.850		

heterozygosity (Table 2). Genetic diversity (*A*, H_T, P_{GT}) also tended to decrease with altitude in both areas, although these patterns were not statistically significant (Fig. 3, Appendix 1).

Population genetic structure

Across both areas, most genetic variation of *S. canadensis* (84%) resided within populations, and relatively little (6%) between mountain areas (Table 3). The variation among populations was rather low (10%) and was almost identical in both areas (1.5% greater in the Valais; Table 3). A similarly low portion of genetic variation of *L. serriola* was attributed to differences between regions (6%). However, populations of *L. serriola* were much more structured genetically than *S. canadensis* (36% of the variation among populations within areas), and this structure was substantially more pronounced in the native than in the introduced area (Table 3).

In the both areas, geographic groups of *S. canadensis* populations explained more genetic variance (2.6%, 0.5% in introduced/native areas, respectively) than altitudinal groups (both areas -0.4%), although both groupings explained very low amounts of variation and this was only significant for geographic groups (east/west) in the Valais ($P < 0.01$). Altitudinal/

geographic groups of *L. serriola* populations explained similar amounts of variation, and larger amounts in the Valais (7.1%, 8.8% altitudinal/geographic groups, respectively in the Valais; -1.2%, 1.5% in the Wallowas), although none of these groupings were statistically significant ($P > 0.09$).

All loci of *S. canadensis* apart from 1B departed significantly ($P < 0.05$) from HWE. All populations departed from HWE through an excess of homozygotes (positive F_{IS}), although this was only significant for nine populations (Table 1). Because the species is an obligate out-crosser, these deviations are most likely explained by the presence of null alleles. Overall, there was no significant difference in the magnitude of excess of homozygosity between areas (Table 2). Genotypic disequilibria were detected between seven pairs of loci involving 19D and 1B. However, excluding linked loci from the AMOVA analyses had only negligible effects on the partitioning of variance (data not shown). All loci of *L. serriola* deviated significantly ($P < 0.001$) from HWE, and all populations had an excess of homozygotes (Table 1, Appendix 1). Indeed, heterozygosity was extremely low in both areas (mean $H_O = 0.04$).

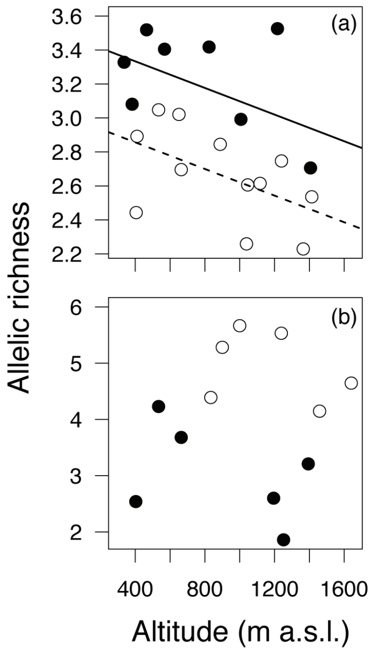


Fig. 3. Relationship between allelic richness and altitude in populations of (a) *Solidago canadensis* and (b) *Lactuca serriola* in the native (filled circles, solid line) and introduced (open circles, broken line) areas. R^2 for the multiple regression models are 0.66 for both (a) and (b) (see Appendix 1).

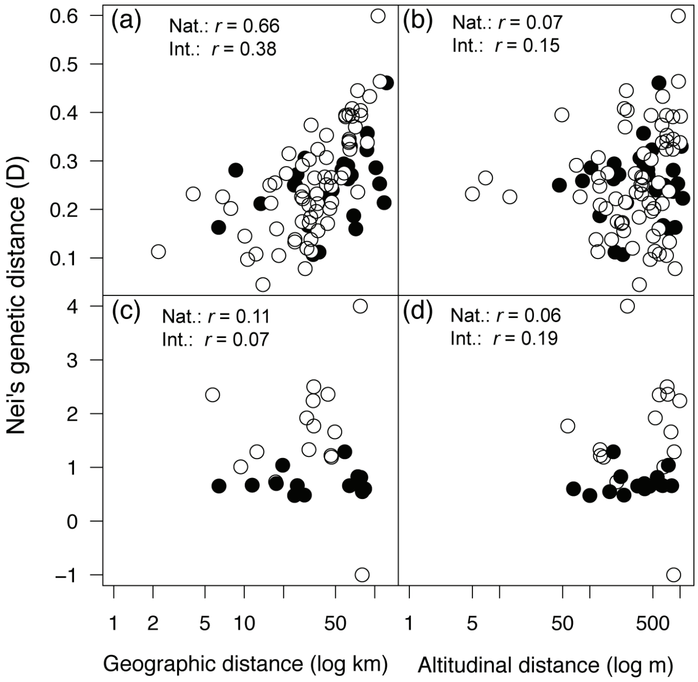


Fig. 4. Relationship between Nei's (1972) genetic distance and geographic/altitudinal distances between pairs of populations, respectively, for *S. canadensis* (a, b) and *L. serriola* (c, d) in the native ("Nat"; filled circles) and introduced ("Int"; open circles) areas.

Genetic distance and geographical structure

Mean genetic distance (*D*) between pairs of populations of *S. canadensis* in the native (mean, SD; 0.259, 0.000) and introduced (0.252, 0.000) areas were not significantly different (Students-t = 0.36, df = 74, $P = 0.7$). Populations were significantly isolated by geographical distance in both areas, although this effect was stronger in the Valais ($Z = 27.5$, $r_M = 0.66$, $P < 0.001$) than in the native area ($Z = 11.8$, $r_M = 0.38$, $P < 0.05$; Fig. 4). The correlation between altitudinal and genetic distances was stronger in the introduced area but these relationships were not significant in either area (native area: $Z = 18.2$, $r_M = 0.07$, $P > 0.3$; introduced area: $Z = 42.9$, $r_M = 0.15$, $P = 0.08$).

Native and introduced populations of *S. canadensis* formed distinct clusters in the UPGMA tree, although bootstrap support for this split was weak (43%; Fig. 5a). Geographically close populations in the Valais tended to group together (e.g. populations Sc3 and Sc8, populations Sc11 and Sc12), although some (e.g. populations Sc2 and Sc10) were genetically more distant from their nearest geographic neighbours. In the native range, there was an approximate north-south divide between clusters of populations. Populations Sc13, Sc15 and Sc19 formed one cluster, and the four most southerly populations another. Interestingly, there was strong bootstrap support for the grouping of the high-altitude populations Sc16/Sc14 and the low-altitude populations Sc18/Sc20 (Fig. 5a). The average distance between populations within these groups (35.6 km) is much greater than the average distance between the pairs of high/low altitude populations (7.5 km; Fig. 1).

Mean genetic distances between pairs of populations of *L. serriola* in the native area (1.639, 0.079) were significantly greater than mean distances between populations in the introduced area (0.712, 0.003; Student's t = 3.23, df = 15, $P < 0.01$). Isolation by distance was stronger in the native area, although not statistically significantly in either area (native area: $Z = 38.1$, $r_M = 0.11$, $P > 0.3$; introduced area: $Z = 16.9$, $r_M = 0.07$, $P > 0.4$). The altitudinal distance between populations was more strongly correlated with genetic distance in the introduced area, although again these correlations were not significant (native area: $Z = 66.2$, $r_M = 0.06$, $P > 0.4$; introduced area: $Z = 26.9$, $r_M = 0.19$, $P > 0.2$).

Native and introduced populations of *L. serriola* were also separated by the UPGMA cluster analysis, although the native population Ls5 was genetically closer to the introduced

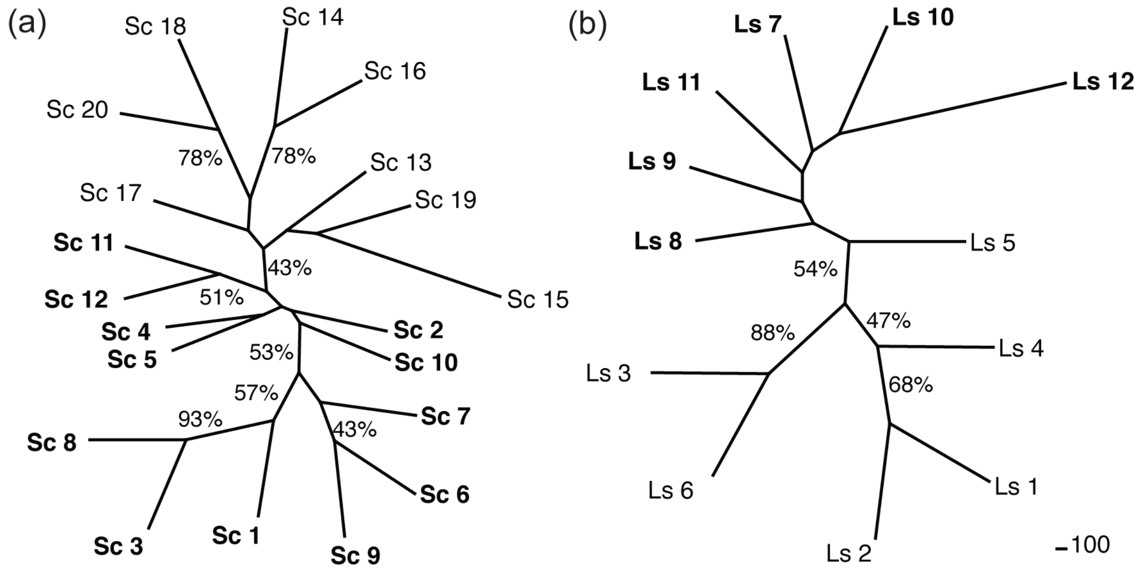


Fig. 5. Unrooted trees from UPGMA cluster analysis based on Nei's (1972) genetic distance between populations of (a) *Solidago canadensis* and (b) *Lactuca serriola*. Branch lengths are scaled relative to the distance between populations. Bootstrap values based on consensus trees are displayed when a node is supported by greater than 40% of 1000 trees. Populations from the introduced range are indicated in bold type.

populations (Fig. 5). The clusters within the native area were generally well supported. The central Valais populations Ls1, Ls2 and Ls4 were united, although strongest support was found for the clustering of the two most geographically distant populations, Ls3 and Ls6. There was very low bootstrap support (< 40%) for groups in the introduced area.

Discussion

Levels of genetic diversity in the mountain areas

A reduction in allelic diversity when populations pass through a genetic bottleneck, either due to sudden reductions in population size or due to colonisation events, is predicted to be a common phenomenon for alien species introduced to a new range (Novak and Mack 2005). The two species in this study showed strongly contrasting differences between levels of neutral genetic variation in the introduced and native areas. The reduction in genetic diversity of populations of *S. canadensis* in the Valais compared to the native area, and in particular the loss of rare alleles, is symptomatic of a founder effect. Because *S. canadensis* was deliberately introduced on a few occasions as an ornamental species (Weber 1994), it is likely that the bottleneck we observed in the Valais is typical of the rest of Europe. However, the effect might be exacerbated in the Valais, where gene flow is primarily restricted by the high flanking mountain chains to east-west movements along the Rhône valley.

Because most genetic variation in highly inbred species is partitioned among rather than within populations, bottlenecks due to founder effects are more common for inbred than for out-crossing species (Chaboudez 1994, Bossdorf et al. 2005 and references therein, Edwards et al. 2006). Therefore, our discovery of higher levels of genetic variation in *L. serriola* in the Wallowas than in the Valais is unusual, although greater within-population genetic variation in the new range is commonly observed for both selfing and out-crossing species (e.g. Novak and Mack 1993, Squirrell et al. 2001, DeWalt and Hamrick 2004, Genton et al. 2005).

Higher recombination rates between individuals, indicated by the greater observed heterozygosity, could explain the greater richness of distinct multilocus genotypes of *L. serriola* in the Wallowas. However, because the degree of inbreeding (F_{IS}) was not significantly different between areas, this diversity is likely to also result from the admixture of multiple source populations from the native range. This explanation is consistent with the history of diverse weed introductions across western North America, especially those associated with agricultural activities (Forcella and Harvey 1988), and has been suggested for other plant invasions in this area, including *Bromus tectorum* (Novak and Mack 1993), *Capsella bursa-pastoris* (Neuffer and Hurka 1999) and *Crupina vulgaris* (Garnatje et al. 2002). However, a similar pattern might also arise if Wallowa populations of *L. serriola* stem from a source area in Europe with substantially more genetic variation than the Valais, and so our results should only be extrapolated to the wider range of the species with caution.

Changes to population structure during mountain invasions

Patterns of population structure and genetic distances between populations were very similar in both areas for *S. canadensis*, as expected for an obligately out-crossing species for which most genetic variation is found within populations (Novak and Mack 2005). Nonetheless, we observed a stronger geographic structuring of populations in the introduced than in the native area, expressed as a slightly higher between-population component of genetic variance, greater bootstrap support for clusters of populations and stronger isolation by distance in the Valais. Greater isolation between populations might be explained by repeated founder events during colonisation of temporary ruderal habitats (Chauvet et al. 2004), and is consistent with the relatively recent origin of the *S. canadensis* invasion in the Valais (i.e. restricted gene flow among isolated founder populations).

In contrast to this situation, *L. serriola* shows much weaker population structure in the introduced area, which might in part be attributed to a higher out-crossing rate. The lower differentiation between populations than in the Valais argues against the multiple introduction of distinct lineages into the Wallowas. It rather suggests that populations in the Wallowas stem from a common, richer gene pool of admixed populations that invaded the area once (or several times from areas with similar genetic compositions) and subsequently spread, as has been suggested for other species (e.g. Kolbe et al. 2004, Genton et al. 2005).

The lack of differentiation between populations of *S. canadensis* along the altitudinal gradients in both areas indicates that these populations are not isolated by barriers to gene flow - due for example to altitudinal variation in phenology or pollinator activities - as has been hypothesised for other species (Wen and Hsiao 2001, Reisch et al. 2005, but see Bingham and Ranker 2000). The connectivity between high/low altitude populations in the native range suggests that any potentially detrimental effect of gene flow on local adaptation will not prevent *S. canadensis* from invading its full altitudinal range in areas where it has been introduced (Garant et al. 2007).

The absence of an altitudinal population structure is less surprising in the case of *L. serriola*, for which gene flow between populations is very low and relatively independent also of the geographic distance between populations. For species such as this, the ecological amplitude of populations could indeed be enhanced by additional gene flow into isolated populations, by increasing the fitness of individuals and exposing greater genetic variation to selection (Holt et al. 2005, Heliyanto et al. 2006). It is thus intriguing that the upper altitudinal limit of *L. serriola* in the Wallowas is c. 500 m higher than in the Valais, despite the close climatic similarity of these regions (Chapter 1), and that this is associated with greater genetic variation and reduced differentiation of populations in this area.

Relationship between altitude and genetic diversity

Analogous with bottlenecks on introduction to a new range, populations spreading along environmental gradients (e.g. during post-glacial recolonisation) also undergo reductions in genetic variation and increased differentiation due to drift (e.g. Chauvet et al. 2004). The same applies to small and isolated populations at the periphery of the core distribution of a species, such as those towards the altitudinal limit (Lesica and Allendorf 1995, Frankham 1996). Both these phenomena might explain the observed decline in genetic variation approaching the altitudinal limit of *S. canadensis*. Other studies involving non-alpine species have also reported declining genetic diversity with altitude (Semagn et al. 2001, Young et al. 2002, but see Gämperle and Schneller 2002), though studies involving mainly alpine species typically report either no clinal variation, or else increasing genetic diversity with altitude (i.e. decline in diversity towards the lower range margin; e.g. Bingham and Ranker 2000, Pleuss and Stöcklin 2004, Reisch et al. 2005).

Populations of *L. serriola* did not decrease significantly in genetic variation with altitude in either area, perhaps due partly to insufficient power to detect significant relationships. However, levels of variation within individual populations of this species might be more contingent on the size and diversity of their founding gene pool than on gene flow among neighbouring populations along environmental gradients. This would be especially so given the short-lived ruderal nature of *L. serriola* populations (Chauvet et al. 2004, Hooftman et al. 2006).

Implications for plant invasions of mountains

The ability of populations to adapt to local environmental conditions is enhanced at intermediate levels of gene flow that permit increased genetic variation but not genetic swamping by maladapted genes (Garant et al. 2007 and references therein). The initial establishment and subsequent invasion of a species should thus be promoted where these conditions are met, potentially leading to the evolution of "invasiveness" (Ellstrand and Schierenbeck 2000, Kolbe et al. 2004). If adaptation is important for spread along environmental gradients, the slight increase in isolation between populations of the out-crossing *S. canadensis*, in contrast to decreases in isolation between populations of the inbreeding *L serriola*, might have promoted their invasion into the mountain areas, even if introduced populations experienced bottlenecks (Frankham 2005).

The close genetic affinity of sometimes quite remote populations also indicates the importance of long-distance anthropogenic dispersal, for example during commercial activities, for the distribution of both species in the Valais. As an example, the Täsch population (Sc1) of *S. canadensis* in the Mattertal appears to have been founded from a source in the central Valais around Sierre (Sc8), as apposed to Visp (Sc9) which is at the mouth of the Mattertal. This can account for the rapidity of some invasions that do not rely purely on natural dispersal. It also suggests that propagule pressure is unlikely to be a major limitation to the spread of alien species within mountain regions, at least in anthropogenically disturbed areas.

Our results clearly demonstrate that plant invasions in mountain areas are not necessarily associated with genetic bottlenecks. Furthermore, the loss of allelic diversity of *S. canadensis* in the Valais has apparently not affected its ecological amplitude along altitudinal gradients. Indeed, the highest population sampled in the Valais (1414 m a.s.l.) corresponds to the highest elevations at which the species can be found in its native range in eastern North America (see Methods). Neutral and quantitative measures of genetic variation are weakly correlated for several reasons (see Reed and Frankham 2001). Thus, assuming variation in quantitative traits is related to the ecological range of a species (Hoffmann and Blows 1994), we would not expect reductions in allelic diversity during a bottleneck to necessarily reduce ecological amplitude. Consequently plant invaders might be expected to colonise the full ecological range as found in their native range, even if they experience population bottlenecks.

However, a contrasting scenario is presented by *L. serriola*. The correlation between the genetic variation of *L. serriola* and its altitudinal range in these mountain areas suggests that its ecological amplitude might indeed be enhanced by increasing genetic variation. Such a situation is most likely to arise for a species exhibiting strong population differentiation in its native range, when individuals from several source populations come together in the introduced range (Taylor and Keller 2007). Given these conditions, it might be possible for an alien species to transgress the niche constraints that operate in the native range (Holt et al. 2005, Broennimann et al. 2007). To test this hypothesis, detailed studies are required to quantify the link between genetic variation and the ecological amplitude of alien species along environmental gradients.

ACKNOWLEDGEMENTS

We are much indebted to Claudia Michel and Daniel Schlaepfer for help with lab work, and to Chris Kettle, Walter Durka, Alex Widmer and Sophie Karrenberg for discussions during the preparation of the manuscript. John Semple kindly determined the *S. canadensis* specimens. Special thanks are due to Clemens van de Weil of Plant Research International, Wageningen, for providing the primers for *L. serriola*, and to Catherine Parks and the La Grande Forestry and Range Laboratory for providing support in the Wallowa Mountains. This work was funded by a grant of the Swiss National Science Foundation to HD.

LITERATURE CITED

Amsellem, L., J. L. Noyer, T. Le Bourgeois, and M. Hossaert-McKey. 2000. Comparison of genetic diversity of the invasive weed *Rubus alceifolius* Poir. (Rosaeceae) in its native range and in areas of introduction, using amplified fragment length polymorphism (AFLP) markers. Molecular Ecology **9**:443-455.

Aradhya, K. M., D. Mueller-Dombois, and T. A. Ranker. 1993. Genetic structure and differentiation in *Metrosideros polymorpha* (Myrtaceae) along altitudinal gradients in Maui, Hawaii. Genetical Research **61**:159-170.

Arévalo, J. R., J. D. Delgado, R. Otto, A. Naranjo, M. Salas, and J. M. Fernandez-Palacios. 2005. Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspectives in Plant Ecology, Evolution and Systematics **7**:185-202.

Bingham, R. A., and T. A. Ranker. 2000. Genetic diversity in alpine and foothill populations of *Campanula rotundifolia* (Campanulaceae). International Journal of Plant Science **161**:403-411.

Bossdorf, O., H. Auge, L. Lafuma, W. E. Rogers, E. Siemann, and D. Prati. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia **144**:1-11.

Broennimann, O., U. A. Treier, H. Müller-Schärer, W. Thuiller, A. T. Peterson, and A. Guisan. 2007. Evidence of climatic niche shift during biological invasion. Ecology Letters **10**:701-709.

Chaboudez, P. 1994. Patterns of clonal variation in skeleton weed (*Chondrilla juncea*), an apomictic species. Australian Journal of Botany **42**:283-295.

Chauvet, S., M. van der Velde, E. Imbert, M. L. Guillemin, M. Mayol, M. Riba, M. J. M. Smulders, B. Vosman, L. Ericson, R. Bijlsma, and B. E. Giles. 2004. Past and current gene flow in the selfing, wind-dispersed species *Mycelis muralis* in western Europe. Molecular Ecology **13**:1391-1407.

DeWalt, S. J., and J. L. Hamrick. 2004. Genetic variation of introduced Hawaiian and native Costa Rican populations of and invasive tropical shrub, *Clidemia hirta* (Melastomataceae). American Journal of Botany **91**:1155-1162.

Dietz, H., and P. J. Edwards. 2006. Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology **87**:1359-1367.

Dong, M., B.-R. Lu, H.-B. Zhang, J.-K. Chen, and B. Li. 2006. Role of sexual reproduction in the spread of an invasive clonal plant *Solidago canadensis* revealed using intersimple sequence repeat markers. Plant Species Biology **21**:13-18.

Edwards, P. J., D. Frey, H. Bailer, and M. Baltisberger. 2006. Genetic variation in native and invasive populations of *Erigeron annuus* as assessed by RAPD markers. International Journal of Plant Science **167**:93-101.

El Mousadik, A., and R. J. Petit. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. Theoretical and Applied Genetics **92**:832-839.

Ellstrand, N. C., and K. A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proceedings of the National Academy of Science (U.S.A.) **97**:7043-7050.

Elphinstone, M. S., G. N. Hinten, M. J. Anderson, and C. J. Nock. 2003. An inexpensive and high-throughput procedure to extract and purify total genomic DNA for population studies. Molecular Ecology Notes **3**:317-320.

Excoffier, L., G. Laval, and S. Schneider. 2006. Arlequin ver 3.01: an integrated software package for population genetics data analysis. Available from: <http://cmpg.unibe.ch/software/arlequin3>.

Excoffier, L., P. Smouse, and J. Quattro. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: Application to human mitochondrial DNA restriction data. Genetics **131**:479-491.

Felsenstein, J. 2006. PHYLIP: phylogeny inference package version 3.66. Available from: <http://evolution.gs.washington.edu/phylip.html>.

Forcella, F., and S. J. Harvey. 1988. Patterns of weed migration in northwestern U.S.A. Weed Science **36**:194-201.

Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. Conservation Biology **10**:1500-1508.

Frankham, R. 2005. Resolving the genetic paradox in invasive species. Heredity **94**:385.

Futuyma, D. J. 1998. Evolutionary Biology. 3rd edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Gämperle, E., and J. J. Schneller. 2002. Phenotypic and isozyme variation in *Cystopteris fragilis* (Pteridophyta) along an altitudinal gradient in Switzerland. Flora **197**:203-213.

Garant, D., S. E. Forde, and A. P. Hendry. 2007. The multifarious effects of dispersal and gene flow on contemporary adaptation. Functional Ecology **21**:434-443.

Garnatje, T., R. Vilatersana, C. T. Roché, N. Garcia-Jacas, A. Susanne, and D. C. Thill. 2002. Multiple introductions from the Iberian peninsula are responsible for invasion of *Crupina vulgaris* in western North America. New Phytologist **154**:419-428.

Genton, B. J., J. A. Shykoff, and T. Giraud. 2005. High genetic diversity in French invasive populations of common ragweed, *Ambrosia artemisiifolia*, as a result of multiple sources of introduction. Molecular Ecology **14**:4275-4285.

Goudet, J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available from <http://www.unil.ch/izea/softwares/fstat.html>.

Heliyanto, B., S. L. Krauss, H. Lambers, G. R. Cawthray, and E. J. Veneklaas. 2006. Increased ecological amplitude through heterosis following wide outcrossing in *Banksia ilicifolia* R.Br.. (Proteaceae). Journal of Evolutionary Biology **19**:1327-1338.

Hierro, J. L., J. L. Maron, and R. M. Callaway. 2005. A biogeographical appraoch to plant invasions: the importance of studying exotics in their introduced *and* native range. Journal of Ecology **93**:5-15.

Hoelzel, A. R. 1998. Molecular Genetic Analysis of Populations. 2nd edition. Oxford University Press, New York.

Hoffmann, A. A., and M. W. Blows. 1994. Species borders: ecological and evolutionary perspectives. Trends in Ecology and Evolution **9**:223-227.

Hollingsworth, M. L., and J. P. Bailey. 2000. Evidence for massive clonal growth in the invasive weed *Fallopia japonica* (Japanese Knotweed). Botanical Journal of the Linnean Society **133**:463-472.

Holt, R. D., M. Barfield, and R. Gomulkiewicz. 2005. Theories of niche conservatism and evolution: could exotic species be potential tests? *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species Invasions: Insights into Ecology, Evolution and Biogeography. Sinauer, Sunderland.

Hooftman, D. A. P., J. G. B. Oostermeijer, and J. C. M. den Nijs. 2006. Invasive behaviour of *Lactuca serriola* (Asteraceae) in the Netherlands: Spatial distribution and ecological amplitude. Basic and Applied Ecology **7**:507-519.

Jensen, J. L., A. J. Bohonak, and S. T. Kelley. 2005. Isolation by distance, web service. BMC Genetics **6**: available from: <http://www.biomedcentral.com/1471-2156/1476/1413>.

Kolbe, J. J., R. E. Glor, L. R. Schettino, A. C. Lara, A. Larson, and J. B. Losos. 2004. Genetic variation increases during biological invasion by a Cuban lizard. Nature **431**:177-181.

Lebeda, A., I. Dolezalova, E. Kristkova, and B. Mieslerova. 2001. Biodiversity and ecogeography of wild *Lactuca* spp. in some European countries. Genetic Resources and Crop Evolution **48**:153-164.

Lee, C. E. 2002. Evolutionary genetics of invasive species. Trends in Ecology and Evolution **17**:386-391.

Lesica, P., and F. W. Allendorf. 1995. When are peripheral populations valuable for conservation. Conservation Biology **9**:753-760.

Mack, R. N., and M. Erneberg. 2002. The United States naturalized flora: largely the product of deliberate introductions. Annals of the Missouri Botanical Garden **89**:176-189.

Nei, M. 1972. Genetic distance between populations. The American Naturalist **106**:283-292.

Nei, M. 1987. Molecular Evolutionary Genetics. Columbia University Press, New York.

Neuffer, B., and H. Hurka. 1999. Colonization history and introduction dynamics of *Capsella bursa-pastoris* (Brassicaceae) in North America: isozymes and quantitative traits. Molecular Ecology **8**:1667-1681.

Novak, S. J., and R. N. Mack. 1993. Genetic variation in Bromus tectorum: comparison between native and introduced populations. Heredity **71**:167-176.

Novak, S. J., and R. N. Mack. 2005. Genet bottlenecks in alien plant species: influence of mating systems and introduction dynamics. *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species Invasions: Insights into Ecology, Evolution and Biogeography. Sinauer, Sunderland, Massachusetts.

Parks, C. G., S. R. Radosevich, B. A. Endress, B. J. Naylor, D. Anzinger, L. J. Rew, B. D. Maxwell, and K. A. Dwire. 2005. Natural and land-use history of the Northwest mountain ecoregions (USA) in relation to patterns of plant invasions. Perspectives in Plant Ecology, Evolution and Systematics **7**:137-158.

Peakall, R., and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes **6**:288-295.

Pleuss, A. R., and J. Stöcklin. 2004. Population genetic diversity of the clonal plant *Geum reptans* (Rosaceae) in the Swiss Alps. American Journal of Botany **91**:2013-2021.

Pohs, K. 2000. The Wallowa Mountains: A Natural History Guide. Northwest Mountain Works, Portland.

R Core Development Team. 2006. R: A Language and Environment for Statistical Computing, available from <http://www.R-project.org>.

Reed, D. H., and R. Frankham. 2001. How closely correlated are molecular markers and quantitative measures of genetic variation? A meta-analysis. Evolution **55**:1095-1103.

Reisch, C., A. Anke, and M. Röhl. 2005. Molecular variation within and between ten populations of *Primula farinosa* (Primulaceae) along an altitudinal gradient in the northern Alps. Basic and Applied Ecology **6**:35-45.

Rousset, F. 1997. Genetic differentiation and estimation of gene flow from *F*-statistics under isolation by distance. Genetics **145**:1219-1228.

Semagn, K., B. Stedje, and A. Bjornstad. 2001. Analysis of genetic diversity and structure in Ethiopian popultions of *Phytolacca dodecandra* using RAPD. Hereditas **135**:51-60.

Semple, J. C., and R. E. Cook. 2006. Asteraceae. Pages 151-157 Flora of North America Editorial Committee, eds 1993+. Flora of North America North of Mexico. 12+ vols., New York and Oxford.

Squirrell, J., P. M. Hollingsworth, R. M. Bateman, J. H. Dickson, M. H. S. Light, M. MacConaill, and M. C. Tebbitt. 2001. Partitioning and diversity of nuclear and organelle markers in native and introduced populations of *Epipactis helleborine* (Orchidaceae). American Journal of Botany **88**:1409-1418.

Taylor, D. R., and S. R. Keller. 2007. Historical range expansion determines the phylogenetic diversity introduced during contemporary species invasion. Evolution **61**:334-345.

van de Wiel, C., P. Arens, and B. Vosman. 1999. Microsatellite retrieval in lettuce (*Lactuca sativa* L.). Genome **42**:139-149.

Weber, E. 1994. Evolutionary trends in European neophytes: a case study of two *Solidago* species. Universität Basel, Basel.

Weber, E. 1997. Morphological variation of the introduced perennial *Solidago canadensis* L. sensu lato (Asteraceae) in Europe. Botanical Journal of the Linnean Society **123**:197-210.

Wen, C. S., and J. Y. Hsiao. 2001. Altitudinal differentiation and diversity of Taiwan Lily (*Lilium longiflorum* var. *formosanum*; Liliaceae) using RAPD markers and morphological characters. International Journal of Plant Science **162**:287-295.

Wieczorek, A. M., and M. A. Geber. 2002. Microsatellite loci for studies of population differentiation and range expansion in *Solidago sempervirens* L. (Asteraceae). Molecular Ecology Notes **2**:554-556.

Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: Integrating evolution, ecology and conservation biology. Annual Review of Ecology, Evolution and Systematics **36**:519-539.

Young, A. G., J. H. Hill, B. G. Murray, and R. Peakall. 2002. Breeding system, genetic diversity and clonal structure in the subalpine forb *Rutidosis leiolepis* F. Muell. (Asteraceae). Biological Conservation **106**:71-78.

Appendix 1: Multiple regression summaries for the relationship between patterns of genetic variation (*A*, allelic richness; H_T, gene diversity; H_O, observed heterozygosity; F_{IS}, inbreeding coefficient; $P_{GT,}$ proportion unique multilocus genotypes), region (R; native or introduced), altitude (Alt) and their interaction (df = 1 for each). Residual df = 16 for *S. canadensis* and 8 for *L. serriola*. Significant *P*-values indicated by bold type.

		S. canadensis		*L. serriola*	
Measure		*F*	*P*	*F*	*P*
A	Alt	9.07	**0.008**	0.18	0.686
	R	20.71	**0.000**	20.16	**0.002**
	Alt:R	0.06	0.812	0.03	0.878
H_T	Alt	6.68	**0.020**	0.08	0.782
	R	10.09	**0.006**	12.31	**0.008**
	Alt:R	0.11	0.743	0.00	0.946
H_O	Alt	0.13	0.728	0.01	0.919
	R	10.57	**0.005**	6.56	**0.034**
	Alt:R	1.70	0.210	0.52	0.490
F_{IS}	Alt	0.41	0.532	0.04	0.853
	R	0.07	0.790	3.83	0.086
	Alt:R	1.40	0.254	1.41	0.269
P_{GT}	Alt	-	-	0.29	0.603
	R	-	-	35.05	**0.000**
	Alt:R	-	-	0.03	0.867

Chapter 4

Plant invasions along altitudinal gradients: implications for the evolutionary ecology of alien invasive plants

THE CONSERVATISM OF ECOLOGICAL NICHES

One of the most striking outcomes of this thesis is the close resemblances in plant traits and patterns of distribution along altitudinal gradients in both the introduced and native ranges of these species. Given the climatic similarities of the two areas along the gradients, this suggests that plants respond to altitude in a similar way in both regions. Furthermore, the comparability of the maximum altitudes at which we observed most species suggest that the ultimate constraints on the altitudinal distribution (e.g. the physiological or developmental determinants of their upper altitudinal limit) are also constant between regions. These observations can be explained by the concept of niche conservatism (Wiens and Graham 2005).

Niche conservatism has been demonstrated at a range of spatial, temporal and phylogenetic scales. At one extreme, species within clades tend to share ecological characteristics that might reflect phylogenetic constraints on the evolution of particular traits within lineages, or dominant selective gradients during the radiation of the lineage (Prinzing et al. 2001, Silvertown et al. 2006). Other evidence comes from GIS-based palaeo-ecological studies of pollen distribution, which indicate that the climatic envelope of temperate tree species is conserved across glacial cycles (Martinez-Meyer and Peterson 2006). This is reflected by the poleward migration of temperate species following deglaciation, and also in their tracking of more recent changes in climate (Parmesan 2006). Theoretical studies also indicate that natural selection should favour adaptations to remain within the fundamental niche (Holt and Gaines 1992, Holt et al. 2005). Furthermore, niche conservatism is a fundamental assumption of (GIS-based) predictive modelling of species distribution (Peterson 2003, Broennimann et al. 2007). If, as our data suggest, species niches are largely conserved, then the extent of alien species invasions in the new range should be predictable with considerable accuracy from their climatic envelope in the native range. However, how does this conservative force mesh with the wealth of recent evidence for rapid evolution in the new range?

EVOLUTION WITHIN THE NICHE

Evidence for evolution in alien species can be broadly grouped into two categories; (1) evolution of fitness/vigour and (2) clinal adaptation along gradients. Examples in the first category relate primarily to the position of a species within a community and its ability to compete with other species, and include the well-known EICA hypothesis (e.g. Blossey and Nötzold 1995, Blair and Wolfe 2004). Examples in the second group include the establishment of clinal patterns of variation in the new range, in particular in relation to latitude, and relate to the spread of a species in a new area (e.g. Weber and Schmid 1998, Maron et al. 2004). These community and landscape levels can be related, for example if increased fitness/vigour promotes the rapid expansion of a species or spread into a wider range of habitats (Dietz and Edwards 2006). However, these rather different evolutionary processes both operate within the confines of the fundamental niche. That is, although adaptive change is observed, the resultant ecological amplitude does not transgress the constraints of the fundamental niche. This explains the converging clinal patterns between ranges noted in this and other studies, and also the observation that although species do respond adaptively to contemporary climate change, these adaptations are not "novel" for the species and operate within the range of states already recorded for the species (Parmesan 2006 and references therein).

However, overall conservatism of the niche might not necessarily be mirrored by the underlying processes which determine it. An indication of this can be found in the differences we observed in patterns of resource allocation to seeds within capitula along altitudinal gradients (Chapter 2). A possible explanation is that species respond primarily by local adaptation in the native range, but by plasticity in the introduced range. It has been suggested that phenotypic plasticity might be a mechanism to bridge adaptive peaks, with subsequent adaptation in the new environment in the longer term (genetic assimilation; Pigliucci and Murren 2003, Richards et al. 2006). Similarly, Huey et al. (2000) found that converging clines in wing size of *Drosophila subobscura* between its native and introduced ranges were explained by elongation of different wing segments. Thus different genetic pathways can lead to similar overall phenotypes.

Related to this, the altitudinal amplitude of *Solidago canadensis* has been apparently unaffected by a strong bottleneck on introduction to the Valais (Chapter 3). Whereas this could indicate the importance of phenotypic plasticity for coping with altitudinal gradients, it also suggests a weak correlation between allelic variation and traits related to the altitudinal limit. If selection eliminates all variation for traits which determine the fundamental niche boundaries (e.g. the altitudinal limit), then variability in all other traits will have no effect on the niche breadth (Reed and Frankham 2001). Such a mechanism has been proposed to explain range boundaries (Hoffmann and Blows 1994, Bridle and Vines 2007), and could also provide an explanation for niche conservatism more generally. Furthermore, it might explain one of the paradoxes of invasion biology, that even introduced populations which lose substantial genetic variation during founder events are able to invade successfully (Frankham 2005).

EVOLUTION BEYOND THE NICHE

The acceptance in recent years of the pervasiveness of rapid evolution in introduced populations has also led to the fear that "invasiveness" can evolve (Ellstrand and Schierenbeck 2000). However, this concept should be set in a comparative context. Thus the establishment of clinal patterns of adaptation in the introduced range should come as no surprise if this replicates similar patterns observed in the native range. However, many characteristics of invasions should predispose alien species to display niche shifts, enabling them to invade environments and communities off-limits to their ancestral populations. Such shifts could result purely from altered biotic interactions (i.e. shift in the realised niche), or due to evolutionary change (i.e. shift in the fundamental niche).

Theory predicts that evolutionary shifts in the fundamental niche can occur when the rate of population decline in an unfavourable environment is slow enough for emergent adaptations to "rescue" the population from extinction (Holt et al. 2005). This is most likely when the population is introduced to a site not too far outside its fundamental niche, which is likely for alien species, given that most establish within the same latitudinal bands which they occupy in the native range (Sax 2001). Similarly, population decline will be slower given a large founding population, and selection more effective given larger amounts of variation, which might be reflected by the importance of high propagule pressure and multiple introductions for the success of many alien species (Ellstrand and Schierenbeck 2000, Holt et al. 2005, Colautti et al. 2006).

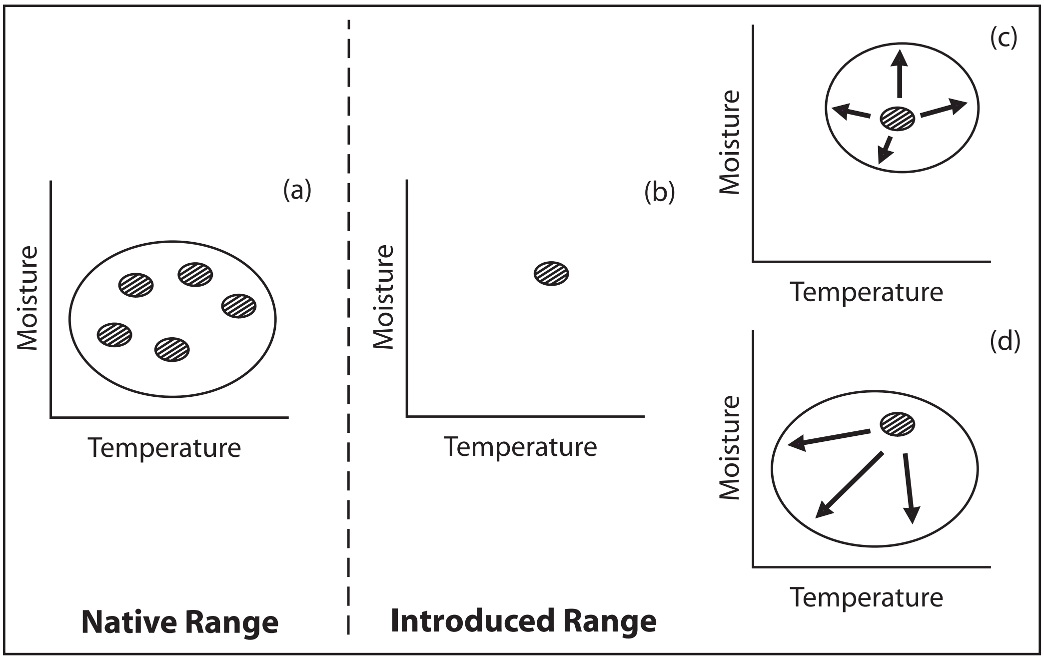


Fig. 1. The fate of the niche in the introduced area. The ellipse in (a) represents the limits of the niche (*sensu* Holt et al. 2005) along two hypothetical niche axes (e.g. temperature and moisture). Hatched ellipses represent locally adapted populations within this niche space. In (b), propagules are introduced to a part of a new range climatically similar to but isolated from their ancestral populations. The population could (c) adapt to conditions along environmental gradients in the new range, so that the observed niche is shifted relative to that in the native range. Alternatively, the niche limits might be conserved between ranges (d), so that adaptation in the new range is confined to the range of environmental conditions within the niche as observed in the native range (niche conservatism). Arrows represent potential adaptive trajectories along environmental gradients.

The failure of peripheral populations to further adapt to conditions beyond the range margin has been explained in part by the swamping effect of gene flow from the range core on emergent adaptations (Kirkpatrick and Barton 1997, Bridle and Vines 2007). This problem can be circumvented in populations of alien species which are isolated from the native range. Furthermore, introduced populations, which are likely to be a biased sample of the native diversity, find themselves at the core of their new distribution in the introduced area (Fig 1). Added to this are the opportunities provided by a mixing of populations from divergent parts of the native range; together with novel selection pressures in the new range, these are likely to increase the probability of niche shifts in alien species (Levin 2003).

Our data indicate that *Cichorium intybus* and *Lactuca serriola* have a wider altitudinal amplitude in their introduced range in the Wallowa Mountains than in the Valais, and in the case of *L. serriola* this is associated with substantially greater genetic variation. Whether or not this constitutes a niche shift remains to be tested. Other evidence for niche shifts come from the failure in particular cases of climate-based models developed in the native range to predict the extent of a species in the introduced range, and vice versa. In two recent examples (Broennimann et al. 2007, Fitzpatrick et al. 2007), the models accurately predict the niche of the first colonists, but not their subsequent spread, suggesting evolution of the niche requirements. However, such models can not distinguish whether any shift is attributed to evolutionary changes in the fundamental niche or ecological changes in the realised niche (Peterson 2003). Shifts in the realised niche of some invaders have been revealed by biological control programmes (e.g. Huffaker and Kennett 1959). *Clidemia hirta* is able to invade forests in its introduced range in Hawaii, from which it is excluded by enemies in the native range and following the introduction of biological control agents (DeWalt et al. 2004). I am not aware of any demonstrations of an evolutionary shift in the fundamental niche of a species.

Following Holt et al. (2005), I have defined the (fundamental) niche as the portion of multivariate niche space within which a species experiences a realised population growth rate greater than one. However, other concepts of the (realised) niche consider not only the response of a species to a given point in niche space, but also its effect on the system and the other organisms in it (Chesson 2000). In this way, an invader which becomes much more abundant in the new range could be said to have shifted its niche, even if environmental constraints on its distribution are unchanged.

IMPLICATIONS FOR INVASIONS ALONG ENVIRONMENTAL GRADIENTS

If the climatic niche of a species is predominantly conserved between ranges, and relatively independent of genetic variation in invading populations, then alien species can be expected to colonise their full ecological extent in the new range. Our data indicate that this can be very rapid, within 100 or so years (see also Jäger 1988). Thus climatic variables, and the need to respond to them, are not major limitations to the spread of alien species, at least within the confines of the fundamental niche.

This conclusion is at odds with observations of the long lag time that often precedes the expansive spread of a species, which has been explained in part by the accumulation of sufficient genetic variation (Ellstrand and Schierenbeck 2000). Furthermore, we have focused on niche axes along mainly abiotic gradients, and neglected the biotic constraints on the realised niche. It is possible that adaptation to the native biota in the new range might exert a considerably stronger constraint on the spread of an invader than abiotic factors. This certainly seems to be the case for the species we investigated which were confined to disturbed sites in the Valais (Chapter 1). Invasion into semi-natural vegetation might be underpinned by the quantity of genetic variation and adaptive potential within populations, or the presence/absence of particular mutualists/enemies in the new range. This might explain why most support for the EICA hypothesis is found among species which have successfully invaded semi-natural vegetation (Dietz and Edwards 2006). However, when considering invasion into semi-natural vegetation it is essential to make comparisons of the ecological amplitude of a species in both the native and introduced ranges. Many aliens are early successional ruderal species which are restricted to disturbed areas, and these would not necessarily be expected to invade into more closed vegetation in the new range (Box 1). A large-scale review of the ecological amplitude of species in both native and introduced ranges has not yet been undertaken.

Future research should focus on the relationship between genetic diversity in introduced populations, their ecological amplitude along environmental gradients and their ability to invade native communities. Investigations of niche shifts in alien species would be particularly valuable for the development of ecological and evolutionary theory, as well as assessing the potential of alien species to invade new communities and of native species to respond to them and to climate change (Levin 2003, Parmesan 2006, Hendry et al. 2007). Niche shifts are at the heart of theories of ecological speciation, and are implicated to explain adaptive radiations of species to exploit divergent habitats, particularly after the colonisation of islands (Francisco-Ortega et al. 1996, Levin 2004). For the reasons outlined above, the processes of island colonisation and biological invasion are very similar. Thus biological invasions along environmental gradients might offer unique opportunities to observe the embryonic stages of ecological speciation (Levin 2003). Herein is contained the irony of invasions: that this great threat to biodiversity might be a source of its creation!

ACKNOWLEDGMENTS

The conceptual framework presented in Box 1 was developed equally by Daniel Schlaepfer and myself during many rewarding discussions.

Box 1. A framework to integrate the ecological changes accompanying the introduction of alien species.

A comparative approach is essential to understand what, if any, ecological changes a species experiences on introduction to a new range. For example, changes in biotic interactions (e.g. due to inferior or "naïve" competitors, enemy release) in the new range can alter the relative abundance of a species at both local and landscape scales. All other environmental factors and propagule pressure being equal, the relative abundance of a species represents the net outcome of its positive and negative biotic interactions. Thus differences in abundance between ranges can be taken as an indication of altered biotic interactions in the new range. Evolutionary changes associated with altered levels of genetic variation within and among populations (e.g. via bottlenecks, admixture, hybridisation) might or might not have ecological consequences in the new range. Similarly, an introduced species might occupy the same or a shifted abiotic niche than in the native range. Thus the ecological changes a species experiences following its introduction to a new range can be characterised within a three-dimensional space

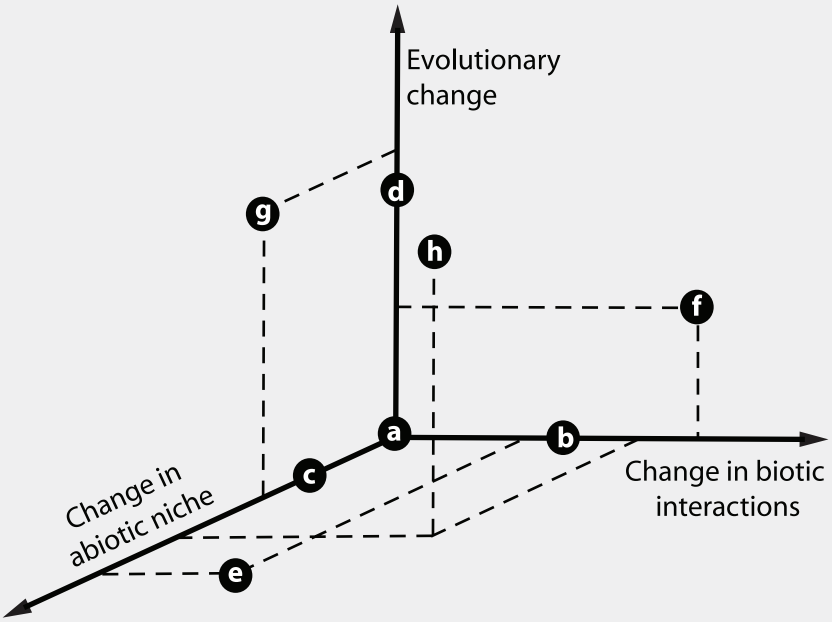


Fig. 1. A conceptual framework to integrate the ecological and evolutionary changes that an alien species can experience on introduction to a new range. Axes represent changes in its biotic interactions, abiotic niche and evolutionary changes relative to the native range. Bullets represent potential scenarios within the space delimited by these axes (see text and Table 1).

delimited by evolutionary changes and changes in its biotic interactions (abundance) and abiotic niche (Fig. 1).

Most species probably experience no considerable change to their ecology on introduction to a new range. Even those considered serious pests in the new range may behave no differently than in the native range, where they are also highly abundant. These would thus be located near the origin of the scheme presented in Fig. 1 (position a). However, release from biotic constraints (e.g. enemy release) might allow some species to achieve greater abundance in the new range, without any evolutionary or abiotic niche changes (Fig. 1, position b). Evolutionary changes occurring within the fundament niche, such as adaptation along climatic gradients, might also have no effects on the relative abundance of a species (position d). Shifts in the abiotic niche of a species can

Table 1. Potential invasion scenarios resulting from changes due to evolution, altered biotic interactions and abiotic niche shifts in the introduced range. Note that other scenarios are possible for each position a-h. Note also that because changes are likely to occur to some degree simultaneously along all three of the axes in Fig. 1, the scenarios encapsulated by positions a-g are oversimplifications. The examples given are thus for illustrative purposes, recognising that in reality the changes experienced by these species will be more complex.

Position	Potential scenario	Example	Reference
a	No ecological change	Many alien species?	
b	Enemy release	Of *Centaurea maculosa* from soil pathogens.	(Callaway et al. 2004)
c	Apparent niche shift due to narrow environmental envelope in native area	Island endemics introduced to continental areas?	
d	Adaptation along environmental gradients	*Solidago* spp. in response to latitude.	(Weber and Schmid 1998)
e	Realized niche shift	*Clidemia hirta* invading Hawaiian forest.	(DeWalt and Hamrick 2004)
f	Evolution of increased competitive ability	*Silene latifolia* in America.	(Blair and Wolfe 2004)
g	Fundamental niche shift	None?	
h	Fundamental niche shift facilitated by increased fitness in new range	None?	(Holt and Gaines 1992)

be explained simply by changes in biotic interactions (i.e. shift in the realised niche; position e), or due to evolutionary changes in the new range (fundamental niche shift; position g) or both (position h). Similarly, evolutionary processes might allow a species to achieve greater dominance within a community relative to the native range (position f). For most alien species, the ecological changes they experience on introduction to a new range will be due to varying extents by simultaneous changes in all three of these dimensions (position h).

The species reported in this thesis were all more common in the new range, suggesting a change in the net outcome of their biotic interactions, and so could be placed at position b. The extent to which their spread along altitudinal gradients is underpinned by adaptive changes would determine their placement at position f. If the greater altitudinal ranges of *Lactuca serriola* and *Cichorium intybus* in the Wallowa Mountains constitutes a niche shift, then these would be placed at position h. However, the extent to which the placement of these (and indeed any) species is determined by additive or interactive effects between the three axes would need to be experimentally determined.

LITERATURE CITED

Blair, A. C., and L. M. Wolfe. 2004. The evolution of an invasive plant: An experimental study with *Silene latifolia*. Ecology **85**:3035-3042.

Blossey, B., and R. Nötzold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology **83**:887-889.

Bridle, J. R., and T. H. Vines. 2007. Limits to evolution at range margins: when and why does adaptation fail? Trends in Ecology and Evolution **22**:140-147.

Broennimann, O., U. A. Treier, H. Müller-Schärer, W. Thuiller, A. T. Peterson, and A. Guisan. 2007. Evidence of climatic niche shift during biological invasion. Ecology Letters **10**:701-709.

Callaway, R. M., G. C. Thelen, A. Rodriguez, and W. E. Holben. 2004. Soil biota and exotic plant invasion. Nature **427**:731-733.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics **31**:343-366.

Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: A null model for biological invasions. Biological Invasions **8**:1023-1037.

DeWalt, S. J., J. S. Denslow, and K. Ickes. 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. Ecology **85**:471-483.

DeWalt, S. J., and J. L. Hamrick. 2004. Genetic variation of introduced Hawaiian and native Costa Rican populations of and invasive tropical shrub, *Clidemia hirta* (Melastomataceae). American Journal of Botany **91**:1155-1162.

Dietz, H., and P. J. Edwards. 2006. Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology **87**:1359-1367.

Ellstrand, N.C., and K.A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proceedings of the National Academy of Science (U.S.A.) **97**:7043-7050.

Fitzpatrick, M. C., J. F. Weltzin, N. J. Sanders, and R. R. Dunn. 2007. The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? Global Ecology and Biogeography **16**:24-33.

Francisco-Ortega, J., R.K. Jansen, and A. Santos-Guerra. 1996. Chloroplast DNA evidence of colonization, adaptive radiation and hybridization in the evolution of the Macaronesian flora. Proc. Natl. Acad. Sci. USA **93**:4085-4090.

Frankham, R. 2005. Resolving the genetic paradox in invasive species. Heredity **94**:385.

Hendry, A. P., P. Nosil, and L. H. Rieseberg. 2007. The speed of ecological speciation. Functional Ecology **21**:455-464.

Hoffmann, A. A., and M. W. Blows. 1994. Species borders: ecological and evolutionary perspectives. Trends in Ecology and Evolution **9**:223-227.

Holt, R. D., M. Barfield, and R. Gomulkiewicz. 2005. Theories of niche conservatism and evolution: could exotic species be potential tests? *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species Invasions: Insights into Ecology, Evolution and Biogeography. Sinauer, Sunderland.

Holt, R. D., and M. S. Gaines. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. Evolutionary Ecology **6**:433-477.

Huey, R. B., G. W. Gilchrist, M. L. Carlson, D. Berrigan, and L. Serra. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science **287**:308-310.

Huffaker, C. B., and C. E. Kennett. 1959. A ten-year study of vegetational changes associated with biological control of Klamath weed. Journal of Range Management **12**:69-82.

Jäger, E. J. 1988. Möglichkeiten der Prognose synanthroper Pflanzenausbreitungen. Flora **180**:101-131.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. The American Naturalist **150**:1-23.

Levin, D. A. 2003. The ecological transition in speciation. New Phytologist **161**:91-96.

Levin, D. A. 2004. Ecological speciation: crossing the divide. Systematic Botany **29**:807-816.

Maron, J. L., M. Vila, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004. Rapid evolution of an invasive plant. Ecological Monographs **74**:261-280.

Martinez-Meyer, E., and A. T. Peterson. 2006. Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. Journal of Biogeography **33**:1779-1789.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics **37**:637-669.

Peterson, A. T. 2003. Predicting the geography of species' invasions via ecological niche modelling. The Quarterly Review of Biology **78**:419-433.

Pigliucci, M., and C. J. Murren. 2003. Genetic assimilation and a possible evolutionary paradox: Can macroevolution sometimes be so fast as to pass us by? Evolution **57**:1455-1464.

Prinzing, A., W. Durka, S. Klotz, and R. Brandl. 2001. The niche of higher plants: Evidence for phylogenetic conservatism. Proceedings of the royal Society of London B **268**:2383-2389.

Reed, D. H., and R. Frankham. 2001. How closely correlated are molecular markers and quantitative measures of genetic variation? A meta-analysis. Evolution **55**:1095 - 1103.

Richards, C. L., O. Bossdorf, N. Z. Muth, J. Gurevitch, and M. Pigliucci. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters **9**:981-993.

Sax, D. F. 2001. Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. Journal of Biogeography **28**:139-150.

Silvertown, J., M. Dodd, D. Gowing, C. Lawson, and K. Conway. 2006. Phylogeny and the hierarchical organization of plant diversity. Ecology **87**:S39-S49.

Weber, E., and B. Schmid. 1998. Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. American Journal of Botany **85**:1110-1121.

Wiens, J.J., and C.H. Graham. 2005. Niche conservatism: Integrating evolution, ecology and conservation biology. Annual Review of Ecology, Evolution and Systematics **36**:519-539.

Acknowledgments

I am very grateful to Peter Edwards and Hansjörg Dietz for supervising my thesis, and to Antoine Guisan for agreeing to be co-examiner.

Peter and Hansjörg offered me the opportunity to take this PhD, and so open a new chapter in my life. The enjoyment and satisfaction I have taken from the last few years, and the opportunities to meet and see wonderful people and places, is due ultimately to them, for which I am always in their debt. I took no greater pleasure than from discussing results and ideas with both Peter and Hansjörg, and this provided me with the motivation which has resulted in this thesis.

I was also extremely lucky to be teamed with Myriam Poll on this project. We always had fun working together in the field, and she was always there when there seemed to be no light at the end of the tunnel.

I am very appreciative of Catherine Parks, Bridgett and Les Naylor, Susan Geer, Elizabeth Venn and all the staff at the Forestry and Range Sciences Laboratory in La Grande, not only for their logistical support in the Wallowas but also for welcoming me into their homes and lives. I will always remember fondly my stay with Bridgett and Les, and thank them for being such wonderful hosts and friends and for not disseminating tales of my truck/cherry stone-related embarrassments beyond the Baker County line. Many thanks also to Paul Kennington for negotiating the sale of our rig.

The Geobot (a.k.a. IBZ) has been a stimulating environment to work in due to all members of the institute. But in particular I would like to thank Karsten Rohweder and Hans-Heini Vogel for coming to the aid of "the master of disaster" on so many occasions, and René Graf and Erika Aeschbach for finding a solution to every technical problem! So also Patrick Cech, who treated my many inane computer queries with such patience, and for warming my heart with his endorsement of Marmite. Many thanks also to Eva Schumacher for sharing her expertise with Adobe CS. I could not list all the people who have contributed along the way, but the many discussions I've had with Daniel Schlaepfer and Christoph Küffer stand out as highlights.

The path through the (mine-) field of statistics was guided by advice from Chris Philipson, Kirk Moloney and Andy Hector, but most of all by Sabine Güsewell to whom I am especially grateful. Alex Widmer, Rolf Holderegger, Regula Billeter, Chris Kettle and Sophie Karrenberg also gave me much valuable advice on the microsatellite study. I am especially thankful to Claudia Michel for showing me the ways of the lab, and to Carmen Rothenbühler, Aria Minder and Daniel Schlaepfer for their help in the lab on many occasions.

I am very grateful for the assistance and company of Sabrina Schmid and Paddy Wallin in the Valais, Susan Geer in the Wallowas and Josephine Haase, Jane and Jesse Alexander whom I press-ganged into counting daisies. My thanks also to Chris Hardy and Donna Ford-Werntz who helped me track-down *Solidago canadensis* in the Appalachians, and especially to John Semple for enlightening the taxonomy of this "tricky" group.

This project was supported financially by the Swiss National Science Foundation and the Stiftung Rübel.

Here I have the privilege to acknowledge the love and support of my family and friends, both old and new. In particular my dearest friend, Josephine Haase, whose patience and kindness in the last months and throughout I can not measure. These people mean more to me than every word of this thesis, and without them not one would have been written.

Curriculum Vitae

Name	Jake Maximillian Alexander
Date of Birth	17th August 1980
Nationality	British

EDUCATION AND QUALIFICATIONS

1999–2003	Biology with a Year in Research, Imperial College of Science, Technology and Medicine, London: 1st Class BSc (Hons). Howarth Prize for excellence in plant science. *Project*: Patterns of resource allocation and size-dependent flowering in seven monocarpic perennials.
1991–1998	A-levels, GCSE; Bristol Cathedral School.

WORK EXPERIENCE

2004–	Scientific assistant/PhD student, Institute of Integrative Biology, ETH Zürich.
Sept.–Nov. 2003	Research assistant, Mammal Research Unit, University of Bristol.
2001–2002	Research assistant, Botany Dept., Natural History Museum, London. *Projects*: molecular/morphological angiosperm systematics, algal biogeography/physiology.
July–Aug. 2000	Research assistant, Imperial College, Silwood Park.

PUBLICATIONS

Alexander, J. M., Edwards, P., Poll, M., Parks, C. and Dietz, H. (in review). Converging responses to altitude in traits of native and introduced Asteraceae forbs. *Ecology.*

Metcalf, J. C. E., Rees, M., **Alexander, J. M.** and Rose, K. (2006). Growth–survival trade-offs and allometries in rosette-forming perennials. *Functional Ecology* **20**: 217-225.

Carine, M. A., **Alexander, J. M.** and Scotland, R. W. (2004). A revision of the *Strobilanthes kunthiana*-group (*Phlebophyllum* sensu Bremekamp) (Acanthaceae). *Kew Bulletin* **59**: 1-25.

Carine, M. A., **Alexander, J. M.** and Russell, S. J. (2003). Evolution of spines and the taxonomic status of *Convolvulus* section Acanthocladi: preliminary results from the ITS2 region of nrDNA. *Bocconea* **16**: 703-710.

CONFERENCE CONTRIBUTIONS

Alexander, J. M., Poll, M., Edwards, P. and Dietz, H. (2007). *Taking the high-road: an intercontinental comparison of plant invasions along mountain roads*. Plant Population Biology Section, Gesellschaft für Ökologie (GfÖ), 17th–19th May. Basel, Switzerland (oral).

Alexander, J. M., Poll, M., Edwards, P., Parks, C. and Dietz, H. (2007). *How do alien plants get high?* Special workshop: Colonization versus invasion: do the same traits matter? 26th February–1st March. Ascona, Switzerland (oral).

Alexander, J. M., Poll, M., Edwards, P., Parks, C. and Dietz, H. (2006). *Variation in reproductive traits of invasive Asteraceae forbs along pronounced elevational gradients in two temperate mountain systems*. Plant Population Biology Section, Gesellschaft für Ökologie (GfÖ), 24th–27th May. Halle, Germany (oral).

Alexander, J. M., Poll, M., Edwards, P., Parks, C. and Dietz, H. (2005). *Reciprocal analysis of ecological and genetic factors of alien plant invasions along altitudinal gradients in the Swiss Alps and the Wallowa Mountains*. Gesellschaft für Ökologie (GfÖ), 19th–23rd September. Regensburg, Germany (poster).